

## Bidrag till Skånes Flora.

### 45. Some phytogeographical aspects of the Scanian flora.

By H. WEIMARCK.

(Meddelanden från Lunds Botaniska Museum, N:r 95.)

An investigation of the flora within so small an area as the province of Scania (Skåne), the southernmost province of Sweden, has brought out certain ecological features which in some cases have general applicability and in others only local. As is well known, plant species with a large area of distribution are often composed of a few to several ecologically different races of which perhaps only one or two are represented within a small area. It is thus clear that in many cases the following discussion is applicable only to Scania and neighbouring areas but not to other parts of the world. Hardly any Swedish province contains within its boundaries such pronounced differences with regard to its nature as Scania. The reasons for the sharp contrasts are:

Its soils are very different in localities at short distances from one another;

Its topography changes from a few metres to 200 metres or more above sea level;

Its climate gives variations in rainfall and different durations of the vegetative period.

**Soils.** North Scania, a triangle with its base along the northern border and its apex near the lake of Ringsjön, is covered with moraines which mainly derive their origin from Archaean rocks. Soils richer in lime are found in small patches only. The streaks of diabase which run through especially the northeastern part of the province have a prominent influence. Soils from the Archaean rocks are mainly acid and poor in nutritious substances.

Eastern Scania, the Kristianstad plain, is covered with soils containing a certain amount of lime (Kristianstad chalk). Material from Archaean rocks that has been transported by the ice from the north-

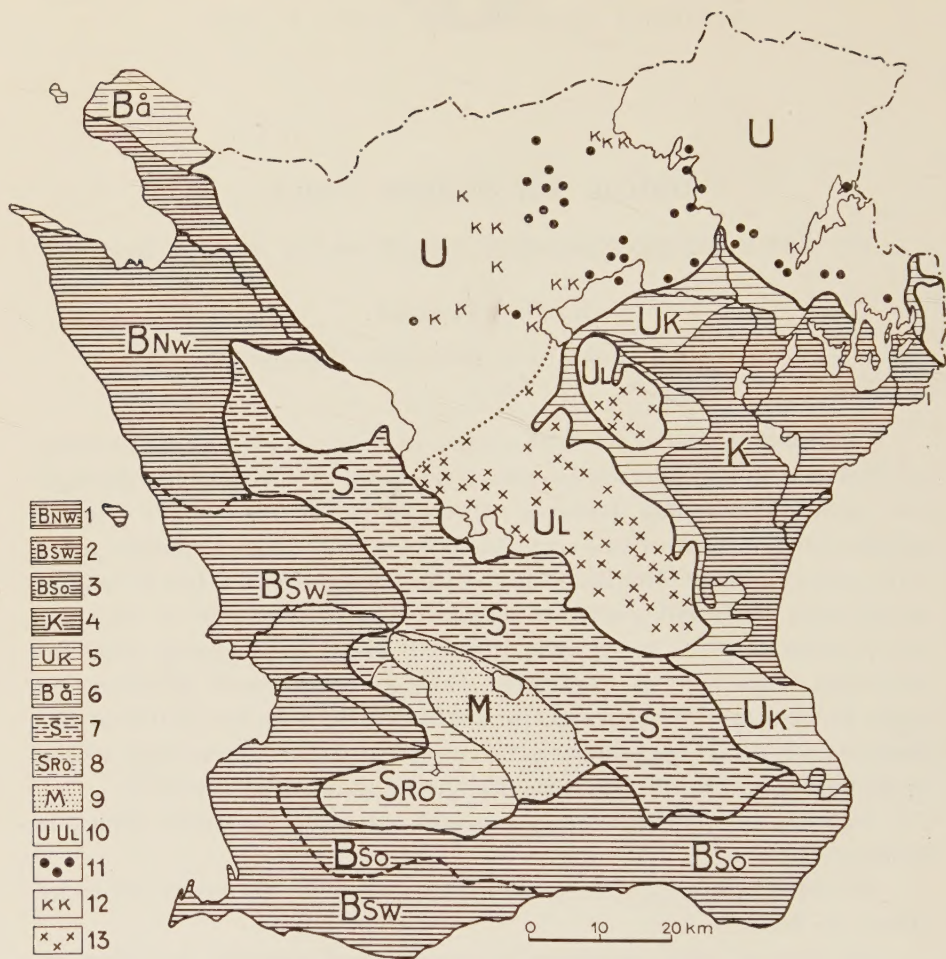


Fig. 1. Areas of soils within Scania. The map is drawn by Dr. WALDHEIM in his work on the dwarf-moss societies of the province (Bot. Not. Suppl. I: 1, 1947). — 1. Baltic N.W. area. 2. Baltic S.W. area. 3. Baltic S.E. area. 4. Kristianstad area. 5. Archaean rock - cretaceous area. 6. Båstad area. 7. Schist area. 8. Schist area of the Romeleåsen. 9. Fine-sand plain. 10. Archaean rock area. 11. Deposits of cretaceous soils within area 10. 12. Deposits of kaolin within area 10. 13. Areas with underlying moraines  $\pm$  rich in cretaceous soils (lime) within area 10.

east has also contributed to the building up of the soils, which are neutral or alkaline in their reaction. Areas with acid soil are also found.

The ridges known as Nävlingeåsen and Linderödsåsen have soils mainly from the substratum of Archaean rocks but lime from the



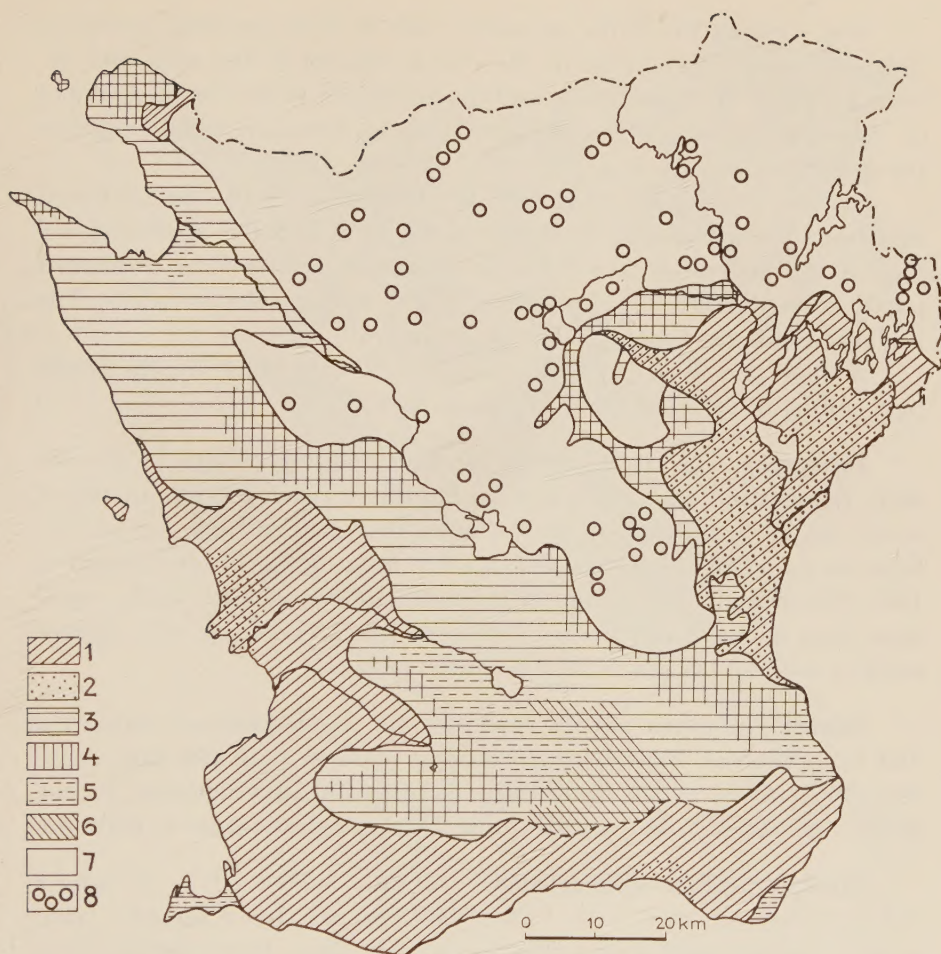


Fig. 2. Map of soil reaction of Scania. The map is drawn by Dr. WALDHEIM (see Fig. 1). — 1. Areas with predominantly subneutral soils (pH 7.0—8.0). 2. Acid sabulous soils (leached) within the preceding areas. 3. Areas with predominantly subneutral soils (pH 6.0—6.9). 4. Parts with numerous acid soils within area 3. 5. Acid sabulous soils (leached) within area 3. 6. Parts with relatively numerous soils slightly alkaline within area 3. 7. Areas with almost exclusively acid soils (pH 4.0—5.9). 8. Scattered localities with subneutral reaction within area 7.

Kristianstad area constitutes a greater or smaller part. The soil reaction is acid at the surface but often changes with greater depth to alkaline. The same applies to the western part of the Hallandsås, the soils of which have a greater or less intermixture of lime from the Båstad area.

The areas of the Baltic moraines, rich in lime and clay, comprise S. Scania from Simrishamn in the east to Malmö in the west and W. Scania west of the Romeleåsen and the Söderåsen to the southern slopes of the Hallandsåsen. The amount of lime is, however, not so high in the northwest.

An area running in a S.E. to N.W. direction as a 10—20 km broad belt from Smedstorp and Benestad to Kågeröd and the north-western part of the Söderåsen is covered by moraines, which have originated partly from Cambro-Silurian schists, partly from Archaean rocks. The soil reaction is here mainly acid or subneutral.

A small area west of the Romeleåsen has soils which for the larger part consist of material from Archaean rocks.

**Topography.** The larger part of N. Scania, Nävlingeåsen, Linderödsåsen, Romeleåsen, Söderåsen and Hallandsåsen reach more than 100 m above sea level. Its highest points, more than 200 m high, are on the Söderåsen and the Hallandsåsen; a large area of the Linderödsåsen is 150—200 m high. The plains in the east, south and west rarely reach more than some tens of metres above sea level. There are often abrupt borders between the plains and the »high land».

**Rainfall.** The larger part of North Scania, Linderödsåsen, Söderåsen and Hallandsåsen, have a yearly rainfall of more than 700 mm, more than 400 mm of which come during the period of vegetation. In the plains the rainfall is less and drops in the south-west corner to 500 mm.

**Phytogeographical differentiation.** Areas having a higher situation above sea level are, as we have already seen, mainly covered with soils primarily poor in lime, their surface layer being leached on account of the high precipitation, in several cases strongly podsolized. The vegetation is for the most part composed of species adapted to an environment poor in nutriment: the species are oligotrophic or acidophilous.

The lower areas and plains on the other hand have, as a rule, fine-grained soils rich in lime and electrolytes from the beginning; they have a lower precipitation, and they get nutritious substances via surface and subsoil waters from the higher areas. Furthermore, in these areas, frosty nights are fewer, snow remains a shorter time on the ground, the vegetative period is longer, and the species are mainly eutrophic or calciphilous and are more southerly or warmth-demanding.



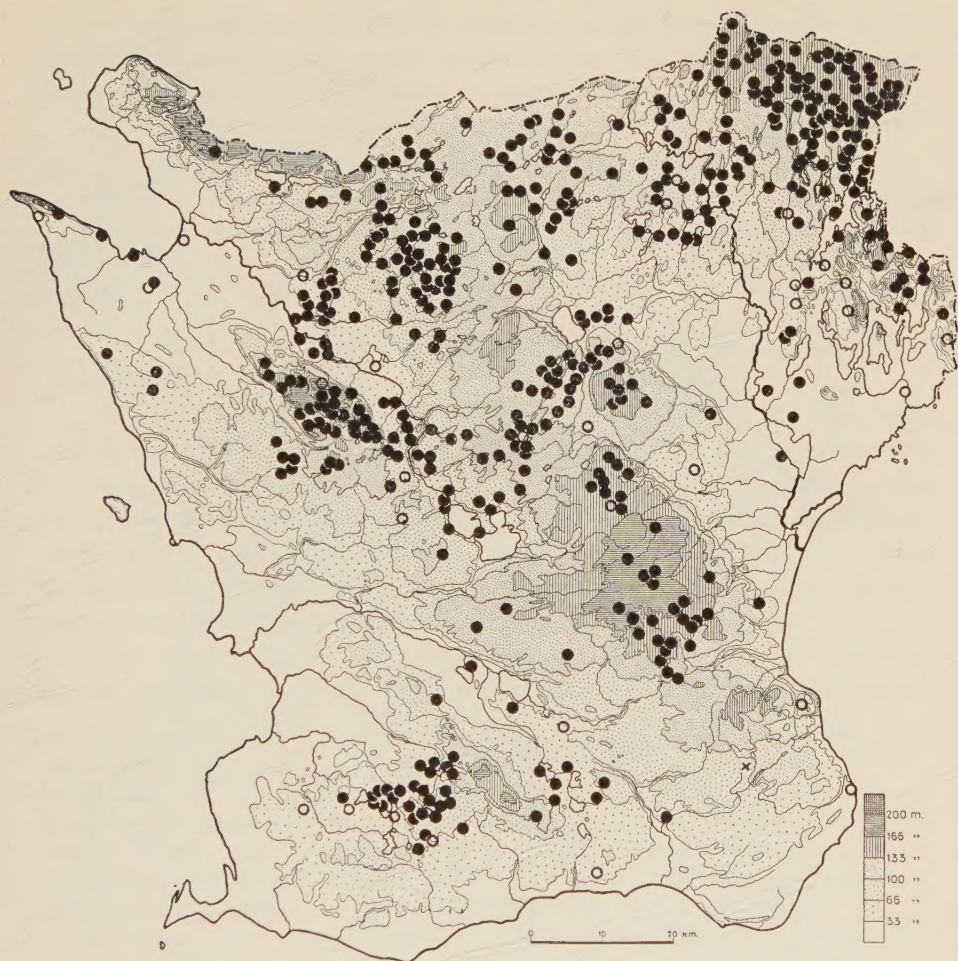


Fig. 3. Distribution map of *Eriophorum vaginatum*, especially characteristic of raised bogs and poor fens. (The field work is not finished, but the distribution type is clear.) The species is common in areas with acid soils (Fig. 2). — Here and in the following maps open rings represent old finds not verified in later time; crosses are old finds where only the name of the parish is known.

We have thus found Scania differentiated into two different areas: one poorer and one richer.

**Forests.** Heath forests are prevalent in those areas of Scania which are covered with moraines exclusively or for the larger part composed of material from Archaean rocks. In the north-east the spruce,

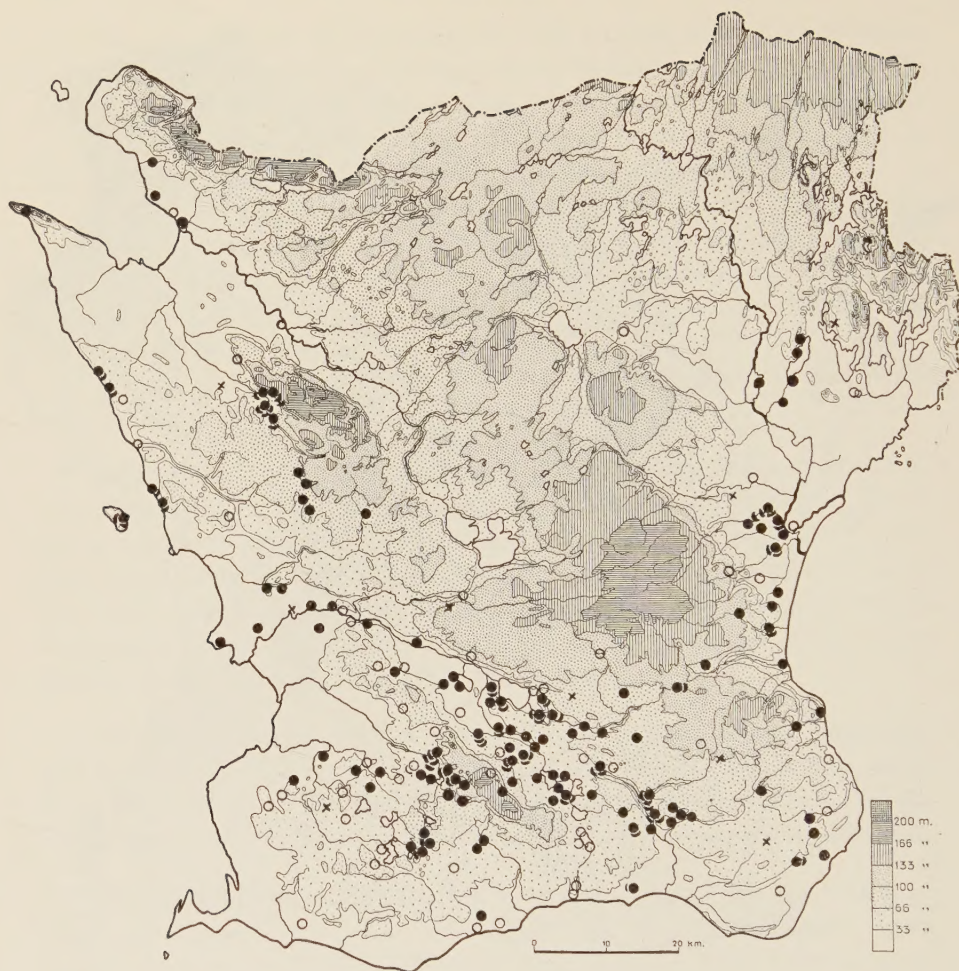


Fig. 4. Distribution map of *Hypericum tetrapterum*, a species occurring only in Scania within Sweden. The species is restricted to fens (wells) rich in lime.

*Picea excelsa*, is a dominant forest tree from the boundary to Blekinge in the east to Fagerhult in the west, an area about 50 km long in an east-westerly direction and 30 km broad. *Picea excelsa* most often forms mixed forests together with the pine, *Pinus silvestris*. The latter tree seems to reach its southern limit near Höör, about 25 km south of Hässleholm. It was cultivated for long periods in other parts, and it is often difficult to judge whether the tree is spontaneous or not.

The oaks, *Quercus petraea* and *Q. Robur*, the beech, *Fagus sil-*



*vatica*, and to a lesser degree the birches, *Betula pubescens* and *B. verrucosa*, are components in the heath forests. *Quercus petraea* is confined to the poorest soils, mainly to pure Archaean rock moraines.

The field layer in the heath forests is very poor in species:

<i>Anemone nemorosa</i>	<i>Linnaea borealis</i>	<i>Pteridium aquilinum</i>
<i>Calluna vulgaris</i>	<i>Lycopodium annotinum</i>	<i>Trientalis europaea</i>
<i>Deschampsia flexuosa</i>	— <i>clavatum</i>	<i>Vaccinium Myrtillus</i>
<i>Equisetum silvaticum</i>	— <i>complanatum</i>	— <i>Vitis-idaea</i>
<i>Goodyera repens</i>	— <i>Selago</i>	

*Hylocomium splendens* and *Pleurozium Schreberi* are the dominating mosses.

**Meadow forests.** The areas with soils richer in lime have forests mainly composed of *Fagus silvatica*, *Fraxinus excelsior*, *Quercus Robur* and *Ulmus glabra*\* *scabra*. The bush layer is often powerfully developed: *Corylus avellana*, *Crataegus monogyna*, *C. Oxyacantha*, *Viburnum Opulus* are here more beautifully developed than in the heath forest, *Cornus sanguinea*, *Euonymus europaea*, *Rhamnus cathartica* and *Ribes alpinum* are found only here.

The field layer is characterized by its richness. The following species are more or less common and are not found in the heath forests:

<i>Agrimonia odorata</i>	<i>Corydalis cava</i>	<i>Neottia Nidus-avis</i>
<i>Alliaria officinalis</i>	— <i>fabacea</i>	<i>Orchis mascula</i>
<i>Allium ursinum</i>	— <i>pumila</i>	<i>Petasites albus</i>
<i>Anemone ranunculoides</i>	<i>Cuviera europaea</i>	<i>Poa remota</i>
<i>Arctium vulgare</i>	<i>Epipactis Helleborine</i>	<i>Primula elatior</i>
<i>Astragalus glycyphylus</i>	— <i>persica</i>	<i>Pulmonaria officinalis</i>
<i>Brachypodium pinnatum</i>	<i>Equisetum hiemale</i>	— <i>obscura</i>
— <i>silvaticum</i>	— <i>pratense</i>	<i>Ranunculus Ficaria</i>
<i>Bromus Benekeni</i>	<i>Festuca gigantea</i>	<i>Rumex sanguineus</i>
— <i>ramosus</i>	<i>Gagea lutea</i>	<i>Sanicula europaea</i>
<i>Campanula latifolia</i>	— <i>minima</i>	<i>Stellaria Holostea</i>
— <i>Trachelium</i>	— <i>spathacea</i>	— <i>nemorum</i> * <i>glochido-</i>
<i>Cardamine flexuosa</i>	<i>Galium odoratum</i>	— <i>sperma</i>
— <i>impatiens</i>	<i>Hypericum hirsutum</i>	<i>Veronica hederifolia</i>
<i>Carex divulsa</i> * <i>Leersii</i>	<i>Lamium Galeobdolon</i>	— <i>montana</i>
— <i>silvatica</i>	<i>Lathyrus vernus</i>	<i>Vicia silvatica</i>
<i>Chaerophyllum temulum</i>	<i>Lunaria rediviva</i>	<i>Viola mirabilis</i>
<i>Circaea intermedia</i>	<i>Mercurialis perennis</i>	— <i>Reichenbachiana</i>
— <i>lutetiana</i>	<i>Myosotis silvatica</i>	

**Heaths and steppes.** These are communities with no tree layer and without or with a low or scattered bush layer. (For more detailed dis-

cussion see O. ANDERSSON, »The Scanian sand vegetation — a survey», this journal pp. 145—172.) The heath vegetation has its home in poor soils, usually with *Calluna vulgaris* as the dominant species; the following species occur here:

<i>Arctostaphylos Uva-ursi</i>	<i>Deschampsia flexuosa</i>	<i>Vaccinium Myrtillus</i>
<i>Calluna vulgaris</i>	<i>Empetrum nigrum</i>	— <i>Vitis-idaea</i>

In sandy soils rich in lime steppe vegetation is the characteristic type. It is most beautifully developed in eastern Scania east of the Linderödsåsen but is also represented in other parts of the province, especially in the south and south-west. Furthermore, its existence depends on a dry, sunny climate.

Above all the following species are represented in this vegetation:

<i>Alyssum Alyssoides</i>	<i>Dianthus arenarius</i>	<i>Medicago falcata</i>
<i>Androsace septentrionalis</i>	<i>Festuca polesica</i>	— <i>minima</i>
<i>Anemone pratensis</i>	<i>Helichrysum arenarium</i>	<i>Minuartia viscosa</i>
<i>Anthericum Liliago</i>	<i>Holosteum umbellatum</i>	<i>Phleum arenarium</i>
— <i>ramosum</i>	<i>Hornungia petraea</i>	<i>Satureja Acinos</i>
<i>Artemisia campestris</i>	<i>Koeleria glauca</i>	<i>Saxifraga tridactylites</i>
<i>Astragalus arenarius</i>	<i>Kohlrauschia prolifera</i>	

An intermediate position between the heath and steppe as delimited above is held by the »*Corynephorus* heath». The soil is here acid but less so than is the case in that of the *Calluna* heath. Among others the following species are found here:

<i>Aira caryophyllea</i>	<i>Helichrysum arenarium</i>	<i>Scleranthus annuus</i>
— <i>praecox</i>	<i>Hypericum humifusum</i>	— <i>perennis</i>
<i>Corynephorus canescens</i>	<i>Jasione montana</i>	<i>Teesdalia nudicaulis</i>
<i>Festuca ovina</i>	<i>Ornithopus perpusillus</i>	<i>Thymus serpyllum</i>

**Moist heaths and meadows.** Between the dry *Calluna* heath and the wet mire comes a transitional type of vegetation as a broader or narrower strip: the moist heath. The soil is acid, often leached and a peat layer is developed.

Soils of this type come into existence in an oceanic climate. A parallel feature is that many species limited to the environment are oceanic—suboceanic:

<i>Arnica montana</i>	<i>Galium hercynicum</i>	<i>Sagina subulata</i>
<i>Blechnum Spicant</i>	<i>Gentiana Pneumonanthe</i>	<i>Trientalis europaea</i>
<i>Cornus suecica</i>	<i>Molinia coerulea</i>	<i>Vaccinium Myrtillus</i>
<i>Deschampsia setacea</i>	<i>Pedicularis silvatica</i>	— <i>Vitis idaea</i>
<i>Erica Tetralix</i>	<i>Radiola linoides</i>	



In the richer parts of Scania the moist heaths are replaced by meadows, which are transitional between the dry steppe and the wet mire. The meadows are very rich in species, but only scattered remnants are left to our times, their area having been reduced so much by man. Among the many species belonging to this vegetation type the following may be mentioned:

<i>Ajuga genevensis</i>	<i>Ophioglossum vulgatum</i>	<i>Potentilla heptaphylla</i>
<i>Betonica officinalis</i>	<i>Ophrys insectifera</i>	— <i>Tabernaemontani</i>
<i>Carex flacca</i>	<i>Orchis incarnata</i>	<i>Pulmonaria angustifolia</i>
— <i>Hartmani</i>	— <i>majalis</i>	<i>Scabiosa canescens</i>
— <i>tomentosa</i>	— <i>militaris</i>	<i>Scirpus compressus</i>
<i>Cirsium acaule</i>	— <i>Morio</i>	<i>Senecio integrifolius</i>
<i>Crepis praemorsa</i>	— <i>sambucina</i>	<i>Serratula tinctoria</i>
<i>Gagea pratensis</i>	— <i>ustulata</i>	<i>Trifolium montanum</i>
<i>Inula salicina</i>	<i>Orobanche major</i>	<i>Vicia tenuifolia</i>
<i>Lysimachia Nummularia</i>	<i>Pimpinella major</i>	<i>Viola hirta</i>
<i>Ononis hircina</i>	<i>Polygala Amarella</i>	

**Mires.** In the areas of Scania with poor soils the mires consist of raised bogs or of poor fens. Only in the north-eastern corner of the province is the surface of the bogs occupied by forest trees: *Pinus silvestris*. This is a continental feature and here we also meet with the continental species *Ledum palustre*, forming a bush layer. In other parts of Scania the surface is open with no or only small and scattered trees. *Erica Tetralix* is a most characteristic species of these more westerly or suboceanic bogs.

Species occurring in the raised bogs are:

<i>Andromeda Polifolia</i>	<i>Drosera rotundifolia</i>	<i>Pinus silvestris</i>
<i>Betula nana</i>	<i>Eriophorum vaginatum</i>	<i>Rhynchospora alba</i>
— <i>pubescens</i>	<i>Erica Tetralix</i>	<i>Rubus Chamaemorus</i>
<i>Calluna vulgaris</i>	<i>Ledum palustre</i>	<i>Vaccinium Oxycoccos</i>

In the north of Scania a fen type is developed called poor fen. Some of its species occur in the raised bogs, some also in the moist heaths. The following species may be mentioned:

<i>Andromeda Polifolia</i>	<i>Erica Tetralix</i>	<i>Rhynchospora alba</i>
<i>Carex magellanica</i>	<i>Eriophorum vaginatum</i>	— <i>fusca</i>
— <i>pauciflora</i>	<i>Myrica Gale</i>	<i>Scheuchzeria palustris</i>
<i>Drosera intermedia</i>	<i>Narthecium ossifragum</i>	

Of these species *Carex magellanica* and *C. pauciflora* are found in no other type of vegetation.

In the rich areas an entirely other type of fen is developed: the



Fig. 5. Distribution map of *Carex pauciflora*. The species is restricted to poor fens. It occurs almost exclusively within the Archaean rock area (Fig. 1) with predominantly acid soils (Fig. 2).

rich fen. The richest type is very rich in species and several rare ones belong to this vegetation type. Often the lime content is so great that calcareous tufa is precipitated. The following species are characteristic:

*Carex acutiformis*  
— *appropinquata*  
— *caespitosa*

*Carex capillaris*  
— *lepidocarpa*  
— *paniculata*

*Carex Pseudocyperus*  
— *riparia*  
*Cirsium oleraceum*



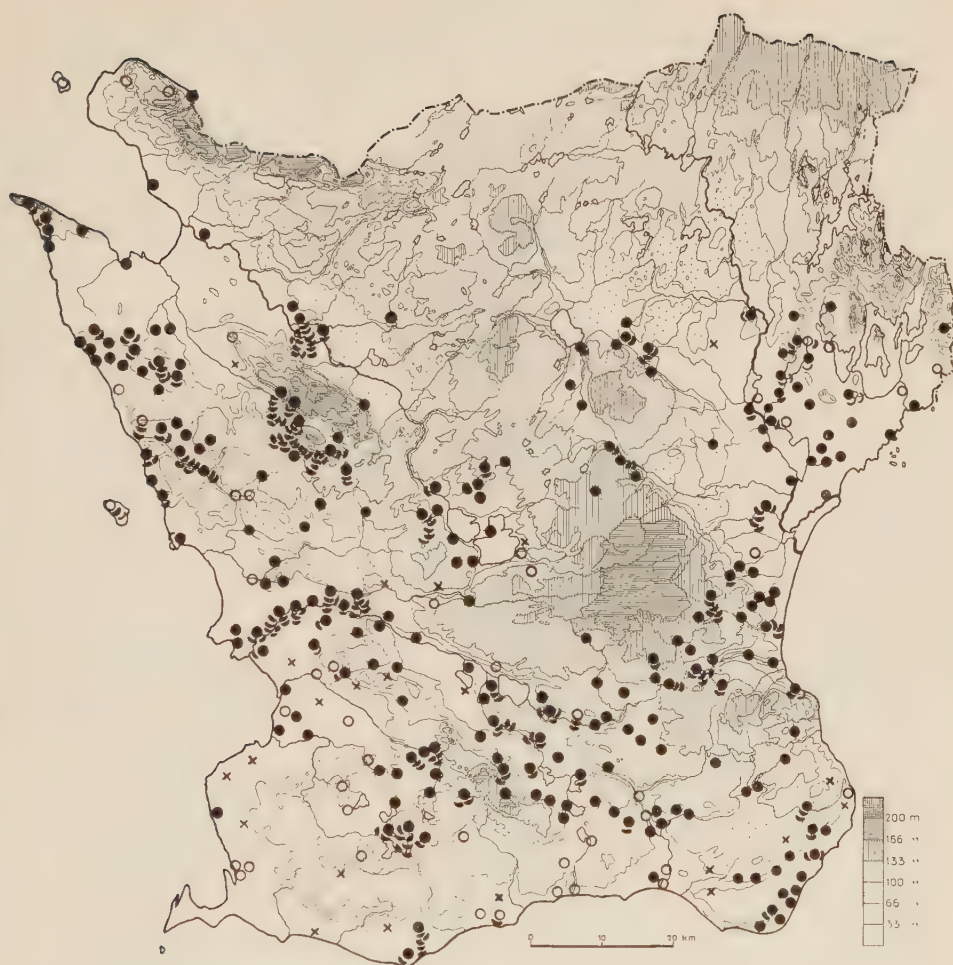


Fig. 6. Distribution map of *Epilobium hirsutum*, a species characteristic of rich fens. It occurs on alkaline or subneutral soils (Fig. 2) and beautifully reflects the distribution of the moraines rich in lime (Fig. 1).

*Epilobium adnatum*

— *hirsutum*

— *parviflorum*

— *roseum*

*Epipactis palustris*

*Euphrasia Rostkoviana*

*Festuca arundinacea*

*Gentiana uliginosa*

*Hypericum tetrapterum*

*Herminium Monorchis*

*Juncus fuscoater*

— *inflexus*

— *subnodulosus*

*Lathyrus palustris*

*Liparis Loeselii*

*Lotus uliginosus*

*Parnassia palustris*

*Rumex palustris*

*Salix rosmarinifolia*

*Schoenus ferrugineus*

— *nigricans*

*Senecio congestus* var. *palustris*

These rich fens had a very much larger distribution in earlier times. To a great extent they have been ditched and changed into cultivated fields and pastures.

**Lakes.** Within the area of the Archaean rock the lakes and running waters are brown and the reaction of the waters is more or less acid. The higher vegetation is composed of a few species only, many of which do not occur in the richer waters:

<i>Isoëtes echinospora</i>	<i>Potamogeton oblongus</i>	<i>Sparganium Friesii</i>
— <i>lacustris</i>	<i>Scirpus fluitans</i>	<i>Subularia aquatica</i>
<i>Lobelia Dortmanna</i>	<i>Sparganium angustifolium</i>	

On the shores of these lakes some species occur which are also found in other oligotrophic types of vegetation, *e.g.* moist heaths and poor fens:

<i>Deschampsia setacea</i>	<i>Myrica Gale</i>	<i>Rhynchospora alba</i>
<i>Gentiana Pneumonanthe</i>	<i>Osmunda regalis</i>	— <i>fusca</i>
<i>Lycopodium inundatum</i>	<i>Radiola linoides</i>	<i>Scirpus multicaulis</i>

The lakes and waters in the rich areas are also much richer in plant species. The following species are confined to such waters or occur also in more or less salt water:

<i>Berula erecta</i>	<i>Potamogeton coloratus</i>	<i>Sium latifolium</i>
<i>Butomus umbellatus</i>	— <i>filiiformis</i>	<i>Spirodela polyrrhiza</i>
<i>Lemna gibba</i>	— <i>panormitanus</i>	<i>Stratiotes aloides</i>
— <i>trisolca</i>	— <i>pectinatus</i>	<i>Veronica Anagallis-aqua-</i>
<i>Mentha aquatica</i>	<i>Ranunculus circinatus</i>	— <i>tica</i>
<i>Oenanthe aquatica</i>	<i>Rumex Hydrolapathum</i>	— <i>aquatica</i>
— <i>fistulosa</i>	<i>Sagittaria sagittifolia</i>	<i>Zannichellia palustris</i>



## The Scanian sand vegetation — a survey.

By OLOF ANDERSSON.

(Meddelanden från Lunds Botaniska Museum, N:r 96.)

In the years 1944—49 I made floristic, sociological, and ecological investigations of the vegetation on the sandy soils of Scania.<sup>1</sup> About 1000 sociological square analyses, *inter alia*, were made. Part of them are tabulated here, with the intention of illustrating both the main types of the sand vegetation and the qualitative as well as quantitative composition of these.

At the analyses a square size of 1 m<sup>2</sup> was used. The degree of cover was recorded according to the Hult-Sernander-Du Rietz scale (DU RIETZ 1921):

5=	the	species	covers	at least	$\frac{1}{2}$	of the square
4=	»	»	»	$\frac{1}{4}$ — $\frac{1}{2}$	»	»
3=	»	»	»	$\frac{1}{8}$ — $\frac{1}{4}$	»	»
2=	»	»	»	$\frac{1}{16}$ — $\frac{1}{8}$	»	»
1=	»	»	»	$\frac{1}{16}$	»	»

In connection with the sociological analyses soil samples were collected and their pH, specific conductance, content of lime (CaCO<sub>3</sub>), mechanical composition, and content of humus determined. I am fully aware that other measurements and analyses should also have been made, for instance measurements of soil temperature, determination of exchangeable Ca, phosphate, *etc.* Thus the analyses made cannot be considered sufficient to throw light upon the conditions of the habitat, but they can give an indication of these. It is not possible, within the compass of this paper, to discuss the ecological problems more in detail. Only a few data will be given. For a more complete

<sup>1</sup> By way of simplification the term sand vegetation is used here but it should be pointed out that the vegetation to be treated of does not occur on pure sand only, but also on mo soils and moraines where as a rule the sand fractions dominate.

understanding of the autecology of the different components cultivation experiments are also advisable.

Docent OVE ALMBORN, Docent GUNNAR DEGELIUS and Dr. A. H. MAGNUSSON have determined or confirmed lichens, Mrs. ELSA NYHOLM and Laborator, Dr. STIG WALDHEIM mosses. To all of them I tender my sincere thanks.

*The Area Investigated.* — The greater part of the sandy shore from Ystad in the south-west to Åhus in the north-east has been investigated. The sandy shore is interrupted between Skillinge and Simrishamn, where the sandstone rock runs out in the sea, and at Stenshuvud and Kivik too.

The area investigated comprises also the still uncultivated and not wood-planted parts of the Kristianstad plain with the adjacent hill-landscape. Certain investigations were made within smaller areas also: within the Ystad-Sandhammaren-area, the Benestad area in the Fyle valley, the Vomb area («the mo plain»), and the Hildesborg-Glumslöv-Ven area.

*Climate.* — The yearly precipitation in the Kristianstad plain averages from 450 to 550 and reaches about 600 mm in the parts adjacent to the Linderöd ridge. The Ystad-Sandhammaren area has an annual precipitation of about 560—590 mm and the Hildesborg-Glumslöv area 500—550 mm (BERGSTEN, 1945).

The temperature stations in the area investigated are few, and the figures for the mean annual temperature are about the same value of all stations. The temperature of juli is 16—17°.

The humidity is comparatively low in the southeastern parts of Scania and in the Kristianstad plain, especially near the coasts. The  $N/(T+10)$  quotient is about 30.

The areas mentioned are both dry and warm, and consequently they favour the occurrence of a termophilous flora and vegetation.

*Topography and Soil Conditions.* — Even if a certain influence on the occurrence of termophilous floral elements in general in the investigated areas can be ascribed to the macro-climate, topography, soil conditions, and biotic factors may nevertheless play a decisive rôle for the differentiation of the main types of the sand vegetation in Scania.

The exposure plays a very great rôle, as anyone with some field experience can easily ascertain, even if he cannot make sure what factor or factors are directly decisive.

The chemical and physical qualities of the substratum are of the greatest importance for the differentiation of the sand-vegetation.



Fig. 1. Hill landscape between Ravlunda and Brösarp. The hills are covered with a vegetation the composition of which varies with regard to soil type, exposure, and so on. The marked hill on this figure is characterized by a meadow grass heath with dominating *Avena pratensis*, *Briza media* and further with *Linum catharticum*, *Chrysanthemum leucanthemum*, *Centaureum minus*, *Leontodon hispidus*. —

Photo: The auth.

The vegetation of the sea-shore and dunes is, as the name indicates, wholly limited to a very narrow belt along the coast. The substratum consists of moving sand with neutral reaction.

The rest of the sand vegetation is to be found on a substratum of rather varying qualities. As regards the character and distribution of the soils in the region of the grass heaths I refer to EKRÖM (1940 and 1950), LINNEMARK (1945), WALDHEIM (1947), and WEIMARCK (1950).

It will only be briefly mentioned that the moraines of the Kristianstad plain are predominantly calcareous. The sand deposits either have



a high content of lime and show an alkaline reaction or are free from lime and show a slightly acid reaction. The soils of the mo plain are as a rule free from lime or slightly calcareous. The soils in the Hildesborg-Glumslöv area belong to the Baltic south-west moraine and are more or less calcareous. The Ystad-Sandhammaren area lies within the region of the Baltic south-east moraine, with both limy and lime-free soils.

### Historical survey.

Already at an early date the sand vegetation attracted the attention of the botanists. Among the 46 species, which JÖRGEN FUIREN and OTTHO SPERLING recorded on their botanical journey through Scania 1623 (1662) they mention *Androsace septentrionalis* from Nymö and a species which they call »*Jacobaea rotundifolia*» and which probably was *Senecio integrifolius* (GERTZ, 1921, ANDERSSON, 1944).

JOHAN LECHE (1744) described *Dianthus arenarius* from Lackalänga and Barsebäck. LINNAEUS mentioned it in his *Flora Suecica* (1745). At that time, however, LINNAEUS had not seen *Dianthus arenarius* in the field. Not until his »Scanian Journey 1749» (1751) did he become personally acquainted with *Dianthus arenarius*; at the same time he discovered several sand plants that were new to the country. He describes his first contact with *Dianthus arenarius* as follows: — »Fragrant fields were stated to be common in summer in the sandy pastures. People said that this delicious odour was particularly noticeable at Midsummer and preferably in the evenings and mornings; they also believed that both rosemary and lavender grew there as in the Spanish fields. When we arrived at the place, we found that all this odour emanated from the flowers of a pink we had never seen further north in this country but afterwards we came across it here in Scania in every sand field, especially among the moving sand, as frequently as the most obnoxious weed.» In the vicinity of Maltesholm LINNAEUS found *Anthericum Liliago* and at Vittskövle, *Astragalus arenarius*. PER OSBECK made a number of excursions in Scania and transplanted some of the characteristic specimens of the Scanian sand flora into his *Hortus Haslöviensis* (GERTZ, 1945).

During his stay at Lund ELIAS FRIES made numerous excursions and found a great many new localities for *inter alia* sand plants (GERTZ, 1928). From WAHLENBERG's diary on his Scanian journey we can derive much information about the Scanian sand flora (GERTZ, 1942).



Fig. 2. Sea slopes between Kåseberga and Löderup. On these a caving-in of the ground occurs. The naked areas are colonized by small mosses, e.g. *Barbula convoluta*, *B. Hornschuchiana*, *Phascum mitriforme*, *P. piliferum*, *Pottia bryoides*, *P. lanceolata* and by therophytes, e.g. *Hornungia petraea*, *Medicago minima*, *Saxifraga tridactylites*, *Kohlrauschia prolifera*. Great parts of the slopes are characterized by a meadow grass heath with *Geranium sanguineum*, *Cynanchum Vincetoxicum*, *Filipendula vulgaris*, *Origanum vulgare* and so on. — Photo: The auth.

Some of the localities he describes very thoroughly, for instance those at Åhus, Degeberga, and Vittskövle.

In his »Bidrag till den Skandinaviska Vegetationens Historia» ARESCHOU (1866) discusses the distribution of the Scanian sand plants.

The only monograph up to now on the Scanian sand flora was published by JOHAN ERIKSSON (1896). His studies mainly deal with the morphology, anatomy, and biology of the sand plants. As an introduction, however, ERIKSSON gives a phytogeographical survey and in this connection makes certain comparisons with the Jutlandish sand



flora, which has been treated of by WARMING. SERNANDER (1920) and STERNER (1922) have touched upon the Scanian sand flora but their primary investigations are only on a small scale.

Attention may also be called to WALDHEIM's (1947) work on mosses and to two smaller monographs by ANDERSSON and WALDHEIM (1946) and by ANDERSSON (1944).

### Terminology.

As designation of the light open more or less dry herbaceous grass vegetation the term grass heath (German »Grasheide«) is here employed. The term was previously used in Swedish literature (STERNER 1922), though in a more restricted sense. This vegetation has also been designated as herb hillsides (Swed. »örthackar«, HULT, 1885. SERNANDER, 1900), hillside meadow, in Swedish »backäng« (ALMQUIST 1929), dry meadows, in Swedish »torrängar« (STERNER, *loc. cit.*, WEIMARCK, 1943, and other authors), steppe vegetation (ANDERSSON and WALDHEIM, 1946), *Bromion erecti* (ANDERSSON, 1944; ALBERTSSON, 1945; KRUSENSTJERNA, 1945). Grass heath, as well as forest, meadow, mire *etc.*, must be regarded as a geographical concept. As to the German term »Grasheide«, reference may be made to MEUSEL (1939, 1940), who has analysed and motivated the use of this term more in detail.

With regard to the qualitative composition I have distinguished plant communities of medium rank, associations. For the separation of the associations indicator species are used: characteristic species and differential species. The former is a species completely or almost completely confined to one community (BRAUN-BLANQUET, 1928). The latter is a species which appears in one community but which is absent or almost absent in another.

The detailed analyses have then been made with regard to the dominance of certain species in order to get an idea in this way about the local constitution of the vegetation. No subdivision of the associations into sociations has, however, been made. The dominance is probably, at least as regards the vegetation type treated here, often due to chance. Nor have the associations been joined into plant communities of higher rank, for instance alliances, in German »Verbände«. The associations have been named in order to facilitate the description.

## The main types of the Scanian sand vegetation.

Two main types of Scanian sand vegetation are distinguished: the vegetation of the sandy sea-shores and the vegetation of the grass heaths.

The former is divided into two associations, that of the foreshore (*Cakiletum*) and that of the sand dunes (*Ammophiletum*).

The grass heaths are divided into acidic and basic ones. In Scania the acidic grass heath (MEUSEL, 1940) consists of only one association (*Corynephorretum*) whose characteristic species have a sub-oceanic area of distribution. The basic grass heath, which is mainly composed of continental floral elements may be differentiated into two subtypes, the sand grass heath, *Koelerietum* (in the main= STERNER's sarmatian grass heaths), and the meadow grass heath, *Avenetum* (in the main=STERNER's sarmatian dry meadows and hillside grass heaths).

### The association of the foreshore (*Cakiletum*).

On account of very unstable external conditions this community is seldom closed. It generally forms a more or less interrupted border. Its characteristic species are the following typical halophytes: —

*Cakile maritima*

*Minuartia peploides*

*Salsola Kali*

These species often become luxuriant because they are supplied with large quantities of nutrients the seaweeds cast up on the shore at high water. Occasionally this association can also contain *Elymus arenarius* and *Agropyron junceum*. *Cakile maritima*, *Salsola Kali*, and *Minuartia peploides* often form miniature dunes. The latter may also dominate on so-called foredunes, which, however, are as a rule formed by the large dune grasses.

The substratum shows a pH in the proximity of the neutral point. The specific conductance is very high. A few words may be said about the halophytes. They were regarded as xerophytes by older scientists. Later investigations, however, have shown (LUNDEGÅRDH, 1949) that the transpiration in, *inter alia*, *Salsola Kali*, *Minuartia peploides*, and *Cakile maritima* is of the same magnitude as in certain mesophytes, e.g. *Galium Mollugo*.



Table 1. Sand

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Salix repens</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Artemisia campestris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cakile maritima</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eryngium maritimum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Galium verum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hieracium umbellatum</i> .....	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Jasione montana</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lathyrus maritimus</i> .....	—	—	—	—	—	1	1	1	1	1	—	—	—	—	—
<i>Minuartia peploides</i> .....	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Petasites spurius</i> .....	—	—	—	—	—	1	2	1	—	—	—	—	—	—	—
<i>Pimpinella Saxifraga</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Agropyron junceum</i> .....	—	1	—	1	1	—	—	—	1	—	—	—	1	—	—
<i>Ammophila arenaria</i> .....	3	4	5	1	1	4	3	2	2	5	1	1	1	1	1
— × <i>Calamagrostis epigeios</i> .....	1	1	—	1	2	—	—	—	—	—	2	2	3	3	1
<i>Carex arenaria</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Elymus arenarius</i> .....	1	1	1	1	2	1	2	2	1	1	1	2	1	1	1
<i>Festuca rubra</i> var. <i>arenaria</i> ....	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Ceratodon purpureus</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tortula ruralis</i> * <i>ruraliformis</i> ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Peziza ammophila</i> .....	—	1	—	—	1	—	—	—	—	—	1	1	1	1	—
<i>Psilocybe ammophila</i> .....	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1

1—5: Löderup, Löderup's beach, 31/7 1947. 6—10: Maglehem, Friseboda, 15/9 1947. 11—15: Löderup, Löderup's beach 19/6 1947. 16—20: Maglehem, Furuboda,

### The association of the sand dunes (*Ammophiletum*).

This association is wholly confined to the sand dunes along the coast. It comprises different stages, which, however, should not be given special names.

The following are characteristic species of *Ammophiletum*: —

<i>Agropyron junceum</i>	<i>Eryngium maritimum</i>
<i>Ammophila arenaria</i>	<i>Lathyrus maritimus</i>
— — × <i>Calamagrostis epigeios</i>	<i>Petasites spurius</i>
<i>Elymus arenarius</i>	

On the foredunes a pioneer stage is developed, in Scania mostly characterized by *Agropyron junceum*, *Ammophila arenaria* and its hybrid with *Calamagrostis epigeios*, as well as *Elymus arenarius*. Associated with these are *Minuartia peploides*, *Cakile maritima*, and *Salsola Kali*, the presence of which is due to the waves reaching the foredunes when gales are blowing. On the dunes inside the foredunes *Ammophila arenaria*, its hybrid with *Calamagrostis epigeios*, and *Ely-*

## Dune Vegetation.

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	1	2	2	5	4	3	5	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	2	—	3	2	1	2	2
1	1	—	1	—	—	—	—	—	1	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
3	3	3	3	3	5	4	4	3	3	3	5	3	4	4	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	1	2	—	2	1	2	2	1	2	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
1	1	1	1	1	1	1	1	1	—	1	1	—	1	1	—	—	—	—	—	—	—	—	—	—
—	—	—	1	1	1	1	1	1	1	1	1	1	1	1	5	4	3	5	5	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	1	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
—	1	—	—	1	—	1	1	—	1	1	1	1	1	1	1	1	1	1	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

20/7 1947. 21—30: Maglehem, Juleboda 19/6 1947. 31—40: Löderup, Löderup's beach, 31/7 1947.

*mus arenarius* are found in large quantities. *Lathyrus maritimus* can dominate these dunes (table 1, analyses 16—30). Here appear also *Eryngium maritimum*, *Petasites spurius*, and *Festuca rubra* var. *arenaria*. The mobile dunes are wholly free from mosses and lichens but curiously enough certain larger fungi are to be found, which are adapted to the extreme conditions prevailing here, viz. *Psilocybe ammophila*, *Peziza ammophila*, and *Phallus Hadriani* (ANDERSSON, 1950).

At this stage the vegetation covers only part of the soil, one-third to one-half. To the windward the shore is in perpetual motion on account of wind and desiccation. In strong gales the vegetation is thickly overlaid with sand.

On the dunes further in from the shore, the fixed dunes, *Ammophila arenaria* most frequently dominates, though other species can also occur as dominants, for instance *Salix repens* (table 1, analyses 36—40) and *Carex arenaria*. The vegetation covers larger areas. Other species are added, e.g. *Artemisia campestris*, *Galium verum*, *Jasione montana*, *Pimpinella Saxifraga*, *Hypochaeris radicata*, and others. Also



*Calluna vulgaris* and *Cladonia*-species as well as several mosses are seen here. As the fixed dunes are generally planted with fir I have not had the opportunity of studying them in detail.

The substratum has a soil reaction about the neutral point (6.7—7.4) (ANDERSSON, 1950). The electric conductance is considerably lower than that of the foreshore. The content of humus is very low in the foredunes and other mobile dunes, whereas it increases in the fixed dunes. The dune sand in Scania contains no lime, which substance is rather common in the English and Dutch dunes. For this reason the dune vegetation is partly rather poor in species in comparison with that of these countries. In the Dutch dune vegetation there occurs for instance *Phleum arenarium*, which in Scania is wholly confined to the basic grass heath (see below).

### The acidic grass heath (*Corynephoretum*).

This community which is wholly confined to north-western Europe was first described from the Cevennes by BRAUN(-BLANQUET) (1915). Later it has been the object of sociological, ecological, and regional-phytogeographical investigations in special papers as well as in larger monographs of vegetation from Germany, Belgium, France, and Poland (ALLORGE, 1922, KOLUMBE, 1925, JURASZEK, 1928, TÜXEN, 1928, BEHMAN, 1930, VOLK, 1930—1931, LIBBERT, 1933, MEUSEL, 1940).

In Sweden it has not previously been subjected to any detailed investigation, though certain fragmentary floristic and sociological statements have been made (ERIKSSON, 1896, WEIMARCK, 1940, SUNESEN, 1942, ANDERSSON and WALDHEIM, 1946). SUNESEN's (1942) work on *Ornithopus perpusillus* is, I think, the most detailed investigation of *Corynephoretum* in Sweden. His pH analyses also give a certain indication of the chemical composition of the substratum.

In its typical constitution *Corynephoretum* (= *Corynephoretum caescentis typicum*, TÜXEN 1937) shows a strong floristic uniformity all over its area of distribution. All species which constitute *Corynephoretum* in north-western Germany are to be found in Scania too. The characteristic species are the following: —

*Aira caryophylla*  
— *praecox*  
*Corynephorus canescens*  
*Filago minima*  
*Hypochaeris glabra*  
— *radicata*

*Jasione montana*  
*Ornithopus perpusillus*  
*Rumex tenuifolius*  
*Scleranthus perennis*  
*Spergula vernalis*  
*Teesdalea nudicaulis*

(*Hypochaeris glabra* is not included in any of the analyses entered in the table 2.)

Of these, *Corynephorus canescens* and *Carex arenaria* form the pioneers of the community on bare sand. By their widely ramified and deep-going root system they are able to bind the sand. Shortly after the occurrence of bare patches in the sand, for instance deflation hollows in fixed dunes, on flat sand-fields exposed freely to the wind on the coasts, on fallow land, in road cuttings, etc. these species immigrate (see Plate II, above). For a longer or shorter time they then constitute the pioneer stage of the community. After the sand has become sufficiently bound other species will immigrate. Among them mention may be made in the first place of *Aira praecox*, *Filago minima*, *Teesdalea nudicaulis*, *Scleranthus perennis*, *Hypochaeris radicata*, *Rumex tenuifolius*, and *Jasione montana*. Locally appear also *Spergula vernalis* and *Ornithopus perpusillus* which are rare in Scania. A remarkable feature is the high percentage of autumn-germinating annuals.

Besides the aforementioned species of the field layer the community is characterized by a great number of cryptogams, for instance among mosses by *Polytrichum piliferum* and *P. juniperinum*, *Ceratodon purpureus*, and *Rhacomitrium canescens* and among lichens by *Cornicularia aculeata*, *Cladonia furcata*, *rangiformis* and *foliacea* var. *alcicornis*.

Before the community reaches its optimal stage it covers about 5—50 per cent of the soil. By and by, however, all the naked patches of sand become overgrown. The field as well as the bottom layer close up into a continuous plant cover (Plate III, below, table 2). On sandy fallows *Corynephorus canescens* sometimes occurs in slight frequency. It is often wholly absent. In such habitats *Agrostis canina* var. *arida* (table 2, analyses 11—20) and *Festuca ovina* appear instead as dominants, with the configuration of species otherwise characteristic of the community.

A closed field and bottom layer results in a greater formation of humus. The physical and chemical conditions of the soil are altered. *Corynephorus canescens* and *Carex arenaria* decrease in frequency and disappear completely at last. This is the introduction to the retrogressional stage of the community, which can proceed in two directions, partly development into a lichen heath, partly into a *Calluna vulgaris* heath (see Plate IV, table 2, analyses 21—35).

The occurrence of *Corynephorum* is correlated with a substratum having a slightly acid reaction, pH lying between 5.2 and 5.9. The

Table 2. The acidic

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Calluna vulgaris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Achillea Millefolium</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arenaria serpyllifolia</i> .....	—	—	—	—	—	—	—	—	—	1	—	—	—
<i>Artemisia campestris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Campanula rotundifolia</i> .....	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Cerastium semidecandrum</i> ..	—	1	—	—	—	—	—	—	—	1	—	—	—
<i>Filago minima</i> .....	—	—	—	—	1	1	1	1	1	1	1	1	1
<i>Galium verum</i> .....	1	—	1	—	—	—	—	—	—	1	—	—	—
<i>Hieracium Pilosella</i> .....	—	—	—	—	—	—	1	1+	3	2+	1	1	1
— <i>umbellatum</i> .....	—	—	—	—	1	—	1	—	—	1	—	—	—
<i>Hypochaeris radicata</i> .....	—	—	—	—	—	—	—	1	1	1	1	—	—
<i>Jasione montana</i> .....	—	—	—	—	1	—	1	1	1	1	—	—	1
<i>Ornithopus perpusillus</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rumex tenuifolius</i> .....	—	—	—	—	1	1	1	1	1	1	1	1	1
<i>Scleranthus perennis</i> .....	—	—	—	—	1	—	1	—	—	—	1	1	—
<i>Spergula vernalis</i> .....	—	1	1	1	1	1	1	—	—	—	—	—	—
<i>Teesdalea nudicaulis</i> .....	—	—	—	—	—	—	1	1	—	1	—	—	—
<i>Thymus Serpyllum</i> .....	—	—	—	—	1	—	—	—	—	—	—	—	—
<i>Viola canina</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	—
— <i>tricolor</i> .....	1	—	—	1	—	—	—	—	—	—	—	—	—
<i>Agrostis canina</i> var. <i>arida</i> ..	—	—	—	—	—	—	—	—	—	—	5	5	5
— <i>tenuis</i> .....	1	2	1	—	1	1	1	1	1	1	—	—	—
<i>Aira caryophylla</i> .....	—	—	—	—	—	—	—	1	1	1	—	—	—
— <i>praecox</i> .....	—	—	—	—	—	—	—	1	1	1	—	—	—
<i>Carex arenaria</i> .....	—	1	—	—	1	1	1	—	—	—	—	—	—
<i>Corynephorus canescens</i> ....	3	3	3	4	4	4+	5	4	3	5	1	1	1
<i>Luzula campestris</i> .....	—	—	—	—	—	—	—	1	1	—	1	—	—
<i>Ceratodon purpureus</i> .....	—	—	—	—	2	4	1	—	—	—	—	—	—
<i>Dicranum scoparium</i> .....	—	—	—	—	—	—	—	—	—	1	—	—	—
<i>Hypnum cupressiforme</i> .....	—	1	1	—	—	—	—	—	—	—	—	—	—
<i>Polytrichum juniperinum</i> ....	—	—	—	—	1	—	1	1	1	1	1	2	1
— <i>pitiferum</i> .....	1	1	—	1	2	1	1+	2+	2+	1	—	—	—
<i>Rhacomitrium canescens</i> ....	—	—	1	—	1	1	1	—	—	—	—	—	—
<i>Tortula ruralis</i> * <i>ruraliformis</i>	3	1	1	1	—	—	—	—	—	—	—	—	—
<i>Cetraria crispa</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cladonia bacillaris</i> .....	—	—	—	—	—	—	—	—	—	—	1	—	—
— <i>coccifera</i> .....	—	—	—	—	—	—	—	1	1	1	1	1	1
— <i>coniocraea</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	—
— <i>cornutoradiata</i> .....	—	—	—	—	—	—	—	1	1	1	—	—	—
— <i>degenerans</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>Floerkeana</i> .....	—	—	—	—	—	—	—	1	—	—	—	—	—
— <i>foliacea</i> var. <i>alcicornis</i> ...	1	1	—	—	—	—	—	—	—	—	—	—	—
— <i>furcata</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	—
— <i>glauca</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	—
— <i>gracilis</i> .....	—	—	—	—	—	—	—	1	1	—	—	—	—
— <i>mitis</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>muricata</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>pityrea</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>pyxidata</i> .....	—	—	—	—	1	—	—	—	—	—	—	—	—
— <i>rangiformis</i> .....	1	1	1	1	—	—	—	1	1	1	—	—	—
— <i>scabriuscula</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>silvatica</i> .....	—	—	—	—	—	—	—	1	2	1	—	—	—
— <i>uncialis</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>verticillata</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cornicularia aculeata</i> .....	1	—	1	—	—	—	—	—	—	1	—	—	1
<i>Peltigera erumpens</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>rufescens</i> .....	—	—	—	—	—	—	—	1	1	—	—	—	—

1—4: Trolle-Ljunghy, Vanneberga, 5/7 1944. 5—7: Ivetofta, Allarp, 10/7 1944.  
8—10: Ivö, 3 km S of the northern point, 12/7 1944. 11—14: Ravlunda, Flodahus, 26/7



## grass heath.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	5	5	5	5	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
1	1	1	1	1	1	1	—	1	1	—	—	1	—	—	—	—	—	—	—	—	—
1	1	—	1	—	—	—	1	1	1	1	1	1	—	—	—	—	1	1	—	1	1
1	—	—	—	—	—	—	1	1	1	—	1	1	—	—	—	—	—	1	—	—	—
1	1	1	1	1	—	—	1	1	1	—	1	1	—	—	—	—	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	—	—	—	—	1	1	1	2	3
1	—	—	—	—	—	—	1	1	1	1	1	1	—	—	—	—	1	1	—	1	1
—	1	1	1	1	—	—	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—
—	1	1	1	1	—	—	1	1	1	1	1	1	—	—	—	—	—	—	1	1	—
—	—	—	—	—	—	—	1	1	1	—	—	1	—	—	—	—	—	—	1	1	—
—	—	—	—	—	—	—	1	1	1	—	—	1	—	—	—	—	—	—	1	—	—
5	5	4	4	5	5	3	1	1	1	1	1	1	—	—	—	—	—	—	—	1	1
—	1	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
1	1	1	1	1	1	1	1	1	1	1	—	1	1	1	1	1	—	1	—	—	—
—	—	—	1	—	—	—	—	—	—	1	1	—	—	—	—	—	1	1	1	1	1
—	1	—	1	1	1	—	—	—	—	—	—	—	1	1	—	1	1	—	1	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1
—	1	—	5	5	4	3	1	1	1	1	1	1	—	—	—	—	1	1	1	1	1
—	—	—	1	—	1	1	1	—	—	—	—	—	1	1	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
1	1	2	—	—	—	—	1	1	1	1	—	1	1	1	1	1	1	1	—	1	1
—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	1	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—
—	1	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	1	—	—	—	1	—	—	1	1	—	—	—	—
—	1	—	—	—	—	—	1	1	—	—	—	1	1	1	1	1	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—
—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	—	—	—	—	—	5	5	5	5	5	5	5	5	5	5	1	1	1	1	1
—	—	—	—	—	—	—	1	1	1	1	1	1	—	—	1	—	—	—	—	—	—
—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	1	1	1	1	1	1	1	1	1	—	1	1	1	—	1
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

1945. 15—20: Maglehem, Juleboda, 26/7 1945. 21—26: Ravlunda, Haväng, 21/7 1945.  
 27—30: Maglehem, Furuboda, 21/7 1947. 31—35: Ravlunda, Killehusen, 15/7 1945.

electric conductivity lies between 13 and 25. VOLK (*loc. cit.*) states a pH amplitude between 4.7 and 6.4, LIBBERT (*loc. cit.*) 4.8--5.1, and TÜXEN (*loc. cit.*) 5.0--5.3.

VOLK (*loc. cit.*), who has made investigations on soil reaction, grain size, content of water, and local climate attaches the greatest and decisive importance to the soil reaction. In this way he tries to explain the causal connection between a plant community and the pH factor. In this particular, however, I do not concur with him. The occurrence of a community as a whole cannot be explained causally but only with a statistic correlation. Only for separate species is it possible to approach the causal relation between species and substratum by instrumental and experimental investigations. A complete solution of the problem is, however, never attained, as the separate species live in competition. The direct importance of this factor can never be ascertained. In field-ecological questions, then, the correlation between separate species and plant communities on the one hand and the character of the substratum on the other hand must be discussed.

### The basic grass heath.

#### The sand grass heath (*Koelerietum*).

The occurrence of this plant community has been hinted at in publications by ERIKSSON (*loc. cit.*), SERNANDER (1920, 1925), and STERNER (*loc. cit.*), as well as by ANDERSSON & WALDHEIM (*loc. cit.*).

In recent days *Koelerietum* is confined to eastern Scania. Earlier it probably covered larger areas of the calcareous sand fields in the neighbourhood of Rinkaby-Åhus-Vittskövle. But a great part of them are now planted with pine and only small remains of the optimal stage of the community are left in these parts.

It reaches its most beautiful development on the sand fields along the coast immediately north of Vitemölla, on the south-exposed hills in the valley of the river Verkeån from Brösarp to Haväng, on the river Julebodaån at Maglehem, and at Degeberga.

Outside Scania it occurs in a thinned type on Ölandic and Gothlandic sand soils.

The characteristic species of the community are:

*Alyssum Alyssoides*  
*Anthericum Liliago*  
*Astragalus arenarius*  
*Cerastium glutinosum*

*Festuca polesica*  
*Helichrysum arenarium*  
*Hornungia petraea*  
*Koeleria glauca*

*Kohlruschia prolifera*  
*Medicago minima*

*Minuartia viscosa*  
*Phleum arenarium*

Most of them are continental species in the widest sense of the word. If HULTÉN's terminology (1950) is used some of them are East-European-continental, others West-European-continental. Some species are Central-European with a westerly tendency, according to HULTÉN's (*loc. cit.*) terminology subatlantic. *Phleum arenarium*, however, is a typically suboceanic species (HORN AF RANTZIEN, 1945).

Besides these species the community contains a number of species with continental distribution, in common with the meadow grass heath (*Avenetum*): —

*Androsace septentrionalis*  
*Anemone pratensis*  
*Anthyllis Vulneraria*  
*Dianthus arenarius*  
*Holosteum umbellatum*

*Medicago falcata*  
*Poa compressa*  
*Satureja Acinos*  
*Saxifraga tridactylites*  
*Thymus Serpyllum*

As dominants in the field layer occur *Koeleria glauca* and *Thymus Serpyllum*. *Artemisia campestris*, *Galium verum*, and *Sedum acre* occur with a high percentage of constancy, the latter also subdominant. A characteristic feature is the presence of the lime-favoured therophytes *Androsace septentrionalis*, *Cerastium glutinosum*, *C. semidecandrum*, *Hornungia petraea*, *Kohlruschia prolifera*, *Medicago minima*, *Minuartia viscosa*, *Phleum arenarium*, *Holosteum umbellatum*, *Satureja Acinos*, and *Saxifraga tridactylites*, some of which together with *Anemone pratensis* wholly characterize the community in spring.

Both the field and the bottom layer are seldom entirely continuous but are interrupted by larger or smaller patches of sand. These are mainly the result of animal activity, which is a necessary condition if the community is to retain its character. The grazing plays the decisive rôle for the formation of sand patches. The tramping of animals continually loosens the cover of plants, and on the hillsides there are often formed terraces, so-called »sheep-tracks» (see Plate IV). The activity of ants and earth-bees is also of some importance. The exposed soil is colonized partly by therophytes, partly by mosses (WALDHEIM, 1947).

The bottom layer is, in its optimal stage, dominated by *Tortula ruralis* \**ruraliformis*, which is accompanied by other mosses, e.g. *Ditrichum flexicaule*, *Racomitrium canescens* (and, rarely, *Tortella inclinata*) and by a great number of lichens, for instance *Cladonia furcata*, *rangiformis*, *foliacea* var. *alcicornis*, *Cornicularia aculeata*,



Table 3. The basic grass heath.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Alyssum Alyssoides</i> .....	—	—	—	—	—	—	—	—	—	1	1	1	1	1	1
<i>Androsace septentrionalis</i> .....	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1
<i>Anemone pratensis</i> .....	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anthericum Liliago</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anthyllus Vulneraria</i> .....	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Arenaria serpyllifolia</i> .....	—	—	—	1	—	—	—	—	—	1	1	1	1	1	1
<i>Artemisia campestris</i> .....	1	1	1	1	1	1	—	—	—	—	1	1	1	1	1
<i>Astragalus arenarius</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cerastium glutinosum</i> .....	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—
— <i>semidecandrum</i> .....	—	—	—	—	—	1	1	1	1	1	1	1	1	1	1
<i>Dianthus arenarius</i> .....	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—
<i>Erodium cicutarium</i> .....	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Galium verum</i> .....	1	1	1	1	1	1	1	1	1	1	—	1	1	1	1
<i>Helichrysum arenarium</i> .....	—	—	—	—	1	—	—	—	—	—	1	1	1	1	1
<i>Hieracium umbellatum</i> .....	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
<i>Hornungia petraea</i> .....	—	—	—	—	1	—	—	1	—	1	—	1	1	1	1
<i>Kohlruschia prolifera</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1
<i>Medicago falcata</i> .....	—	1	—	—	—	—	1	1	1	2	—	—	—	—	—
— <i>lupulina</i> .....	—	—	—	—	—	—	1	—	1	—	1	—	—	—	1
— <i>minima</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1
<i>Pimpinella Saxifraga</i> .....	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—
<i>Satureja Acinos</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1
<i>Saxifraga tridactylites</i> .....	—	—	—	—	—	—	1	1	1	1	1	1	1	1	1
<i>Sedum acre</i> .....	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1
<i>Thymus Serpyllum</i> .....	1	1	1	1	1	1	1	1	1	1	2+	1	3	2	1
<i>Veronica verna</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1
<i>Viola rupestris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>tricolor</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—
<i>Bromus tectorum</i> .....	—	1	1	1	—	1	—	—	—	—	—	—	—	—	—
<i>Carex arenaria</i> .....	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Corynephorus canescens</i> .....	1	—	1	1	1	—	—	1	—	—	—	—	—	1	—
<i>Festuca polesica</i> .....	—	—	—	—	—	—	1	1	1	1	1	1	1	1	1
<i>Koeleria glauca</i> .....	1	1	1	1	1	1	1	1	3	2	3	3	3	3	5
<i>Luzula campestris</i> .....	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Phleum arenarium</i> .....	1	—	—	1	1	1	1	1	1	1	1	1	1	1	1
<i>Barbula convoluta</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>jallax</i> var. <i>brevirostris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
— <i>Hornschuchiana</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1
— <i>ungiculata</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1
<i>Brachythecium albicans</i> .....	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—
<i>Bryum argenteum</i> .....	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Camptothecium lutescens</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Ceratodon purpureus</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1
<i>Ditrichum flexicaule</i> .....	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Encalypta vulgaris</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1
<i>Hypnum cupressiforme</i> .....	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—
<i>Phascum mitriforme</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
<i>Rhacomitrium canescens</i> .....	1	—	1	1	1	1	1	1	1	1	3	1	1	—	1
<i>Thuidium abietinum</i> .....	1	1	1	1	1	1	—	—	—	—	—	—	—	—	—
<i>Tortella inclinata</i> .....	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—
<i>Tortula ruralis</i> * <i>ruraliformis</i> ..	5	5	5	5	5	5	4	4	4	5	1	1	1	—	1
<i>Bacidia muscorum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cladonia foliacea</i> var. <i>alcicornis</i> ..	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—
— <i>furcata</i> .....	—	—	—	—	—	—	1	1	1	1	1	1	1	1	1
— <i>pyxidata</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
— <i>rangiformis</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—
<i>Cornicularia aculeata</i> .....	1	1	1	1	1	1	1	1	—	—	1	1	1	1	1
<i>Leptogium lichenoides</i> .....	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
<i>Peltigera lepidophora</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>rufescens</i> .....	—	—	—	—	1	—	1	—	—	—	1	1	1	—	—
<i>Toninia coeruleonigricans</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tulostoma brumale</i> .....	1	1	1	1	1	1	1	—	—	—	—	—	—	—	—

The sand grass heath.

[illegible]

SW of the railway station, 2/7 1945. 26—30: Maglehem, near Juleboda, 16/7 1945.

*Peltigera rufescens*, *P. lepidophora*, etc. *Toninia caeruleonigricans*, newly discovered in Scania, also appears locally. The bottom layer is characterized by certain xerophytic fungi, *Tulostoma brumale*, *T. granulolum*, *Disciseda Bovista*, *Geaster nanus* and *minimus* (ANDERSSON, 1950).

If the development of the community is not interfered with, for instance by grazing, a gradual change takes place in its character. In the field layer the lime-favoured therophytes disappear and in the bottom layer *Tortula ruralis* \**ruraliformis* decreases to the benefit of *Rhacomitrium canescens*, which finally appears as dominant. For some time *Rhacomitrium canescens* can appear as dominant in the optimal stage. Sooner or later, however, an immigration of other floral elements takes place, especially of the characteristic species of the *Corynephorum* association, for instance *Corynephorus canescens* (which occasionally can appear in the optimal stage), *Teesdalea nudicaulis*, *Scleranthus perennis*, and *Jasione montana* among the phanerogams. In the bottom layer there appear, of mosses, *Polytrichum piliferum* and *P. juniperinum* and, of lichens, *Cladonia silvatica* and *Cetraria crispa*.

Of the constituents of *Koelerietum Anthericum Liliago*, *Dianthus arenarius* and *Astragalus arenarius* remain for a long time (cf. also JURASZEK 1928, page 588).

On account of the mixture of suboceanic and continental elements, the retrogressional stage just described has been arranged in the »Corynephorion-Verband» by certain Central-European authors (LIBBERT, 1933, KLIKA, 1931). That is probably not correct. The whole of it depends on a soil process which will be briefly described below.

In certain localities, for instance steep, south-exposed hills where the heat is stronger and the evaporation rapid, which prevents leaching, *Koelerietum* can develop in another direction, viz. into a dry meadow grass heath, especially characterized by *Medicago falcata*.

In Scania *Koelerietum* is entirely confined to a sandy substratum characterized by a relatively high content of lime ( $\text{CaCO}_3$ ), varying between 5 and 20 per cent. The soil-reaction is alkaline and shows values between 7.0 and 8.3. The electric conductance varies between 40 and 90.

Soil profiles from habitats with the optimal stage of the community show two horizons only, a humus horizon varying between 10 and 25 cm in thickness and the unaltered mineral horizon showing a pH about 9.0.

Soil profiles in the degeneration stage of the community show three



horizons: a humus horizon from 20 to 30 cm thick, with a pH between 5.8 and 6.5, a rust soil horizon varying between 60 and 85 cm and with a pH between 7.3 and 7.6, and the unaltered mineral horizon.

The cause of the degeneration of the community is thus a soil process, in which numerous changes take place in the surface. This, however, cannot be discussed here. By using a very rough generalization we may say that the process consists in a leaching of the lime and the nutritive salts in the surface.

### The meadow grass heath (*Avenetum*).

It was pointed out above that the sand grass heath may successively pass into a dry meadow grass heath. It may then perhaps appear unjustified to distinguish between these two types. In their extremes, however, they are well separated.

The sand grass heath is in the field layer distinguished by xerophytes and therophytes. In the bottom layer the lichens are a characteristic element. In the meadow grass heath, on the other hand, no or extremely few lichens are contained. It is physiognomically attached to the calcareous moist meadows, with which it has many species in common.

This community has been described, or its occurrence in Sweden has been indicated, by SERNANDER (1908), STERNER (*loc. cit.*), ALBERTSSON (1941, 1945, 1946), ANDERSSON (*loc. cit.*) and ANDREASSON and WALDHEIM (*loc. cit.*).

In Scania the meadow grass heath is most beautifully developed within »the hill landscape of Österlen», in the moraine soils of the Kristianstad plain round the Råbelöv, Oppmanna, Ivö and Levra lakes and on the sea-slopes from the Hammar hills to Löderup and from Hildesborg to Glumslöv and on the island of Ven.

The characteristic species of the community in Scania are:

*Ajuga genevensis*\*

*Avena pratensis*

— *pubescens*

*Campanula glomerata*\*

*Carex obtusata*\*

*Centaureum minus*

*Cynanchum Vincetoxicum* s

*Fragaria viridis*

*Gagea pratensis*\*

*Geranium sanguineum* s

*Helianthemum nummularium*

— *ovatum*

*Melampyrum arvense*\*

*Orobancha major*\*

*Peucedanum Oreoselinum* s

*Phleum phleoides*

*Polygala comosa*

*Potentilla heptaphylla*

— *Tabernaemontani*

*Pulmonaria angustifolia*\*

<i>Ranunculus polyanthemos</i> *	<i>Thalictrum minus</i> *
— <i>bulbosus</i>	— <i>simplex</i>
<i>Scabiosa canescens</i>	<i>Trifolium montanum</i> *
— <i>Columbaria</i>	<i>Veronica spicata</i>
<i>Senecio integrifolius</i>	<i>Vicia tenuifolia</i> s

(The species denoted with s are most nearly attached to the shrub vegetation. Those designated by an asterisk are not included in any analyses, but for excellent reasons they are nevertheless placed among the characteristic species of the community.)

The following species are common with the calcareous moist meadows and form differential species as against *Koelerietum*:

<i>Briza media</i>	<i>Linum catharticum</i>
<i>Carex flacca</i>	<i>Ononis spinosa</i>
<i>Centaurea Jacea</i>	<i>Plantago lanceolata</i>
<i>Cirsium acaule</i>	<i>Polygala Amarella</i>
<i>Daucus Carota</i>	<i>Primula veris</i>
<i>Filipendula vulgaris</i>	<i>Prunella vulgaris</i>
<i>Leontodon hispidus</i>	<i>Viola hirta</i>

Species common with *Koelerietum* and thus differential species as against the calcareous moist meadows have been mentioned at the treatment of *Koelerietum*.

The least hydrophile calcareous moist meadows have the following differential species as against *Avenetum*:

<i>Carex panicea</i>	<i>Orchis militaris</i>
<i>Crepis praemorsa</i>	— <i>Morio</i>
<i>Geum rivale</i>	— <i>ustulata</i>
<i>Herminium Monorchis</i>	<i>Ranunculus acris</i>
<i>Molinia caerulea</i>	<i>Succisa pratensis</i>
<i>Ophioglossum vulgatum</i>	

In comparison with *Koelerietum Avenetum* is richer both in herbs and grasses. The total number of species within *Avenetum* is twice as large as in *Koelerietum*.

The meadow grass heath is characterized by a coherent field layer in which *Avena pratensis* (ANDERSSON 1944), *Briza media*, *Festuca ovina*, *Medicago falcata*, and *Thymus Serpyllum* dominate. Dominance of *Briza media* or *Avena pratensis* and *Festuca ovina* with a strong admixture of *Linum catharticum* and *Carex flacca* represents the wettest type of all, *Medicago falcata* often a somewhat drier type. *Avena pratensis* and *Festuca ovina*, which often appears as dominant in dry calcareous moist meadows, may be dominants in the dry as well as in the moist type.



Above. Foreshore vegetation with *Salsola Kali* and *Cakile maritima*. — Sandhammaren, 1947.

Below. Sand dune vegetation with *Ammophila arenaria* and *A. arenaria* × *Calamagrostis epigeios*. — Löderup's beach, 1947.





Above. Initial-stage of *Corynephorum* with the pioneers *Carex arenaria* and *Corynephorus canescens*. — Ystad, 1945.

Below. Optimal-stage with dominating *Corynephorus*. — Vanneberga, 1944.



Above. Retrogressional stage of *Corynephorum* with invading lichens.  
Haväng, 1945.

Below. Retrogressional stage with invading *Calluna*. -- Killehusen, 1945.





Above. A south-exposed hill characterized by the optimal-stage of *Koelerietum*.  
Kungsmölla, 1945.

Below. *Anthericum Liliago* on a south-exposed hill near Maglehem. — 1947.





Aspect of the sand grass heath in the early summer with flowering *Koeleria glauca*, *Galium verum*, *Dianthus arenarius* and *Sedum acre*. — Kungsmölla, 1946.



Above. Vernal aspect of the meadow grass heath with flowering *Primula veris*, *Anemone pratensis* and *Luzula campestris*. — Kungsmölla, 1946.

Below. Meadow grass heath with dominating *Peucedanum Oreoselinum*. — Ystad, 1946.

Within the drier type of *Avenetum* there are, rarely, some calcareous moist meadow species to be found (see Table IV, the analyses 1—10). On the other hand certain species occur here that reach their highest frequency of individuals within *Koelerietum*. The moister type shows a strongly inclining tendency for these.

The drier type is in the bottom layer distinguished by *Tortula ruralis* \**ruraliformis* and *Thuidium abietinum*. In the moister one there are in addition *Fissidens cristatus* var. *mucronatus*, *Thuidium Philibertii*, etc.

As regards the difference in the bottom layer between the moister *Avenetum* type and the calcareous moist meadow species it may be pointed out that *Fissidens cristatus* var. *mucronatus* is replaced by *Fissidens adianthoides*.

As a rule the meadow grass heath is grazed and then it keeps its specific character. If the grazing ceases, a special type of meadow grass heath gradually develops, distinguished by flora elements that in reality belong to the shrubbery or forest skirts vegetation. The analyses (36—40) in Table IV have been included as instances of this. The constitutive elements of this type are in the first place *Cynanchum Vincetoxicum*, *Geranium sanguineum*, *Peucedanum Oreoselinum* and *Vicia tenuifolia* (cf. BÖCHER, 1945).

In course of time shrubs and other herbs intrude, too. The community develops into a shrubbery vegetation. Among the shrubs may be mentioned *Cornus sanguinea*, *Rhamnus cathartica*, *Prunus spinosa*, *Euonymus europaeus* and *Crataegus* species.

Characteristic species of this vegetation are:

<i>Agrimonia Eupatoria</i>	<i>Hypericum montanum</i>
— <i>odorata</i>	<i>Laserpitium latifolium</i>
<i>Allium scorodoprasum</i>	<i>Lathyrus niger</i>
<i>Astragalus glycyphyllus</i>	<i>Lithospermum officinale</i>
<i>Campanula Cervicaria</i>	<i>Melampyrum cristatum</i>
— <i>persicifolia</i>	— <i>nemorosum</i>
<i>Carex digitata</i>	<i>Picris hieracioides</i>
— <i>montana</i>	<i>Trifolium medium</i>
<i>Chaerophyllum temulum</i>	<i>Vicia cassubica</i>
<i>Clinopodium vulgare</i>	— <i>dumetorum</i>

This community is very instable and if it is not exposed to any culture influence it develops into forest.

What has now been described is one of the directions in which the community may develop. The succession may also take another direc-





The meadow grass heath.

[illegible]

Table 4 (continued).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Senecio Jacobaea</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Silene nutans</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>vulgaris</i> .....	—	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Solidago Virgaurea</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Taraxacum</i> sp. ....	—	—	—	—	—	1	—	1	—	—	—	—	—	—
<i>Thalictrum simplex</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thymus Serpyllum</i> .....	4	5	4+	5	4+	5	5	4+	3	3	3	1	2	1
<i>Veronica spicata</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>verna</i> .....	1	—	—	—	—	—	—	—	—	1	—	—	—	—
<i>Vicia hirsuta</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>tenuifolia</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Viola canina</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>hirta</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Agrostis tenuis</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	2	—
<i>Anthoxanthum odoratum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Avena pratensis</i> .....	1	1	1	—	—	—	—	—	—	—	—	—	—	—
— <i>pubescens</i> .....	—	1	—	—	—	—	—	—	1	—	—	—	—	—
<i>Briza media</i> .....	—	—	—	—	—	—	—	—	—	—	5	3	5	5
<i>Carex caryophylllea</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	—	—
— <i>ericetorum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>flacca</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dactylis glomerata</i> .....	—	—	—	—	1	—	—	—	—	1	—	—	—	—
<i>Festuca ovina</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— <i>rubra</i> .....	3	1	2	2	2	1+	1	1	1	1	1	—	—	—
<i>Luzula campestris</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Phleum phleoides</i> .....	2	1	1	1	1	2	1	1	2	1	—	—	—	—
<i>Poa compressa</i> .....	—	—	—	—	—	—	—	1	—	—	—	—	1	1
— <i>pratensis</i> .....	1	1	—	—	—	—	—	1	—	1	—	—	—	—
<i>Aloina rigida</i> .....	—	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Barbula convoluta</i> .....	1	1	1	1	1	1	1	1	1	1	—	—	—	—
— <i>jallax</i> .....	—	—	—	1	1	1	—	1	1	—	1	1	1	1
— <i>Hornschuchiana</i> .....	1	1	1	1	1	1	1	1	1	1	—	—	—	—
— <i>rubella</i> .....	—	—	—	—	1	—	1	1	—	—	—	—	—	—
— <i>unguiculata</i> .....	—	—	1	1	1	—	—	—	1	—	1	1	1	1
<i>Bryum argenteum</i> .....	1	1	—	1	—	—	—	—	1	—	—	—	—	—
— sp. ....	—	—	—	1	—	1	—	—	—	—	1	—	—	—
<i>Camptothecium lutescens</i> .....	1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Campylium chrysophyllum</i> .....	1	1	1	1	—	—	—	—	1	—	1	1	1	1
<i>Ceratodon purpureus</i> .....	—	—	—	—	1	1	—	—	1	—	—	—	—	—
<i>Ctenidium molluscum</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Distichium capillaceum</i> .....	—	—	—	—	—	—	—	—	—	—	—	1	—	—
<i>Ditrichum flexicaule</i> .....	—	1	—	—	1	—	1	—	—	—	—	—	—	—
<i>Encalypta vulgaris</i> .....	1	1	1	1	1	1	1	1	1	1	—	—	—	—
<i>Eurhynchium Swartzii</i> * <i>rigidum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Fissidens cristatus</i> * <i>mucronatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hypnum cupressiforme</i> .....	1	—	1	—	—	—	—	—	1	—	—	—	—	—
<i>Phascum curvicolle</i> .....	1	1	—	—	1	1	1	—	—	—	—	—	—	—
— <i>piliferum</i> .....	—	—	—	—	—	—	—	—	1	1	—	—	—	—
<i>Pottia lanceolata</i> .....	1	1	1	1	1	1	1	1	1	1	—	—	—	—
<i>Thuidium abietinum</i> .....	4	3	5	3	5	4	3	2	3	1+	—	—	—	—
— <i>Philibertii</i> .....	—	—	—	—	—	—	—	—	—	—	1	1	1	1
<i>Tortula ruralis</i> * <i>ruraliformis</i> ..	1	1	1	1	1	1	1	1	1	1	—	—	—	—
— <i>subulata</i> .....	—	—	—	—	—	—	—	—	—	—	—	—	1	1
<i>Collema pulposum</i> .....	—	—	—	—	—	1	1	1	1	—	—	—	—	—
<i>Nostoc</i> sp. ....	1	1	—	1	1	1	1	1	1	—	—	—	—	—

1—10: Trolle-Ljungby, Knutehus, 10/6 1944. 11—15: Ravlunda, 1.5 km WNW of the church, 21/7 1945. 16—20: Ravlunda, 1 km WNW of the church, 11/7 1945. 21—25: Benestad, Skvattemölla. 13/6 1946. 26—28: Trolle-Ljungby, Åleboken, 17/6



[illegible]

1947. 29—31: Österslöv, Balsby, 14/6 1944. 32—33: Trolle-Ljungby, Hamrahuset, 10/7 1944. 34—40: Löderup, Löderup's beach, 30/6 1946.

tion, the leaching of the soil surface in this case being of greater importance. The following species are characteristic of this stage:

<i>Agrostis tenuis</i>	<i>Trifolium arvense</i>
<i>Antennaria dioica</i>	— <i>striatum</i>
<i>Calluna vulgaris</i>	<i>Sieglingia decumbens</i>
<i>Carex pilulifera</i>	<i>Viscaria vulgaris</i>

Among mosses *Astomum*, *Weissia microstoma*, *Hylocomium splendens*, *Dicranum scoparium*, etc. may be mentioned.

*Avenetum* appears in Scania on comparatively fine-grained soils in which the »mo» fraction plays an important rôle. The physical condition of the substratum is of differentiating importance for the development of *Avenetum* and *Koelerietum* respectively, because the content of lime, soil reaction and electric conductance are about the same in soils overgrown with these communities.

The meadow grass heath of Scania shows a very great resemblance to the meadow grass heath on gravel ridges in Västergötland and on moraine grounds of Öland and Gotland. Certain of the Scanian characteristic species are lacking, it is true, but on the other hand there are in addition others that are absent in Scania. This might be ascribed to immigration-historical and perhaps also anthropogenous causes.

Characteristic species of *Avenetum* in Öland, Gotland and in Västergötland are the following:

<i>Adonis vernalis</i> (Öl.)	<i>Potentilla rupestris</i> (Vg.)
<i>Dracocephalum Ruyschiana</i> (Vg. and adjacent distr.)	<i>Ranunculus illyricus</i> (Öl.)
<i>Oxytropis pilosa</i> (Gotl., Ög.)	<i>Stipa Joannis</i> (Vg.)

Further comparisons should be made between the basic grass heath of Scania on one side and those of the mentioned provinces on the other. Space and time do not allow of this, and such a comparison must be postponed.

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## Regional studies in North Swedish mire vegetation.

By HUGO SJÖRS.

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### Phytogeographical regions of North Sweden.

**Limes norrlandicus.** The meaning of the concept »North Sweden» is not obvious, but must be defined. From a naturalist's point of view, not only the territory referred to as Norrland but also the NW, more or less elevated part of Svealand, viz. the province of Dalarna and the N parts of the provinces of Västmanland and Värmland, possibly also the Kilsbergen hills in Närke, must be included. The »*limes norrlandicus*» of SERNANDER (cf. M. FRIES 1948) may conveniently be regarded as the S borderline of »North Sweden». It is not a sharp line, but a narrow zone of transition. The *limes* is a border of physical geography,

not only of biogeography (the »biological Norrland limit» in DU RIETZ 1935), and must be recognized through a synthesis from elements of topography, climate, distribution of biocoenoses and of animal and plant species, and perhaps also of some physically determined branches of human activity, e.g. the cultivation of certain plants, etc. We cannot expect a full coincidence of all the elements constituting the *limes norrlandicus*. Nevertheless, we have to draw the line where the change is sharpest. Even if confined to phytogeography, such a synthetic study is very difficult, and we must not blame those who prefer an easily determined though quite artificial line, for instance that connecting the northern outposts of wild *Quercus Robur*, as the borderline between the S and the N coniferous forest region.

**The northern coniferous forest region.** N of the *limes norrlandicus* the region of almost unbroken pine (*Pinus silvestris*) and spruce (*Picea Abies*) forest extends over the whole country with the exception of the Scandes (the Fennoscandian mountains, LJUNGER 1944, 1949) and the upland in the northernmost corner of Lappland. Of course, this extraordinarily broad vegetational belt is not quite homogenous, and there have been many attempts to subdivide it. A differentiation into three chief zones or sub-regions may be convenient in this connection.

The first is a S and SE zone comparatively rich in »South-Scandinavian» plants. This lower sub-region is difficult to define, because most of the southern plants have only scattered occurrences in climatically or edaphically favoured stations, and do not possess a distinct borderline. There are several southern plants that do not prefer such stations and consequently may have a greater value as regional indicators. They are mainly plants of moist or wet ground: *Alnus glutinosa*, *Rhamnus Frangula*, *Myrica Gale*, *Calla palustris*, *Rhynchospora alba*, etc. *Viburnum Opulus* may also be mentioned. Their areas are given in HULTÉN's Atlas (1950). More detailed information is found about Dalarna in ALMQUIST 1949, and about Jämtland in LANGE 1938. However, their areas do not coincide in all parts. They are all common in Bergslagen (the southernmost part of N Sweden, i.e. N Västmanland, S Dalarna, etc.) and have a continuous distribution in Dalarna as far NW as Malung and the valley of Lakes Siljan and Orsasjön, and a varying number of scattered stations NW of this line. In Jämtland, they appear in the E part (with the exception of *Alnus glutinosa*) but *Viburnum*, *Myrica*, and *Rhamnus* are widespread also in the central part. The latter two have stations in central N Lappland as far N as Vittangi and Jokkmokk, respectively, but as a whole, the group is



confined in the N to the vicinity of the coast. Additional species showing about the same type of distribution (HULTÉN's maps) are *Dryopteris spinulosa*, *Lycopodium inundatum*, *Glyceria fluitans*, *Agrostis stolonifera*, *Scirpus silvaticus*, *Rhynchospora fusca*, *Carex gracilis*, *Juncus bulbosus*, *Salix aurita*, *S. repens*, *Polygonum Hydropiper*, *Crassula aquatica*, *Lythrum salicaria*, *Peucedanum palustre*, *Lysimachia vulgaris*, *Myosotis palustris*, *Limosella aquatica*, and some plants preferring cultivated ground, e.g. *Gnaphalium uliginosum*. As to some water plants, cf. SAMUELSSON 1934 pp. 117–149 (»die bottnische Gruppe»; some members of »die lappländische Gruppe», which is »wenig einheitlich»). There are, however, some species that reach far N in the eastern part of Norrland but stop at the *limes norrlandicus* in Bergslagen (*Lathyrus palustris*, *Lastrea Thelypteris*), and also some that do not advance so far N in the Bothnian coastal provinces as the majority (e.g. *Drosera intermedia*), and even some species with an almost W—E northern limit (e.g. *Succisa pratensis*).

If we consult the detailed map in LANGLET (1937 p. 373) of the number of days with a mean temperature of  $+6^{\circ}$  or more, we find that the upper limit of most of these species (if the last-mentioned plants and the more or less isolated outposts of the others are disregarded) corresponds to a duration of the period mentioned of about 145 days in the S but only about 125 days in the N. The summer days are, however, both warmer and longer on the N part of the coast than in places with the same length of the summer in the inland further south. The October temperature map in ÄNGSTRÖM (1946) gives about the same picture as LANGLET's thermoisochrones. A detailed September or Late August map would perhaps give the combination of warmth and duration of the vegetation period in a better way.

WAHLENBERG, who was the first to propose a regional phytogeographical division of N Sweden, distinguished one *Acer* and one *Myrica* region (1826 p. XXXII). As the occurrence of *Acer platanoides* and other plants of climatically favoured habitats is always very scattered, such a division is difficult to carry out. The *Acer* zone would be confined to the coastal belt and lower valleys in the S half of North Sweden and to the districts along the *limes norrlandicus*. The Västerbotten and Norrbotten coast and the uplands in the more southern provinces fall outside this zone (in spite of some scattered *Acer* localities in the latter).

It is obvious that the boundary between the lower and the middle sub-region is subordinate and that it cannot be drawn so distinctly as the *limes norrlandicus*. Cf. ANDERSSON & BIRGER 1912 pp.

27—30. An especially open question is the position of Central Jämtland with its interesting flora rich in southern as well as northern species. It seems perhaps most reasonable to include it in the middle sub-region, or perhaps to let it constitute a sub-region of its own. Its flora is somewhat related to that of the Siljan Cambro-Silurian in Dalarna, which is, however, clearly a part of the lower sub-region.

The middle sub-region is characterized by the more or less abundant occurrence of a number of northern species (HULTÉN's maps) such as *Agrostis borealis*, *Tofieldia pusilla*, *Salix glauca*, *Stellaria calycantha*, *Epilobium Hornemanni*, *E. alsinifolium*, *E. lactiflorum*, *Petasites frigidus*, *Gnaphalium norvegicum*, *Saussurea alpina*, *Lactuca alpina*, etc. Most of these have scattered stations in the lower sub-region, too, but much higher frequency in the middle and upper sub-regions. They are often termed »subalpine species» (or even »alpine») in floristic literature. I think this terminology is to be avoided, because only a minor part of their area falls within the subalpine (or alpine) regions. See esp. the very painstaking maps of the distribution of *Lactuca alpina* by M. FRIES (1949). Some species may be added that are most common on calcareous soil at least outside the Scandes (*Cystopteris montana*, *Carex atrata*, *C. capitata*, *C. Angarae*, *Juncus triglumis*, *Salix Myrsinites*, *Thalictrum alpinum*, *Astragalus alpinus*, *Viola biflora*, *Epilobium davuricum*, *Primula stricta*, *Gentiana nivalis*, *Myosotis silvatica* ssp. *frigida*, *Euphrasia frigida*, *Bartsia alpina*, *Erigeron acre* ssp. *politum*, *E. boreale*). A more special type of distribution is represented by *Aconitum septentrionale* (M. FRIES 1949). The latter group of species is, in fact, as a rule somewhat more concentrated to the Scandes (excepting *Carex capitata*, *C. Angarae*) but their rich occurrence in the Cambro-Silurian Foreland of Jämtland shows that their scarcity elsewhere in the coniferous forest region is mainly a question of unsuitable edaphical conditions. There is also a small group of north-eastern species that are more or less widespread in the middle sub-region, esp. its N part, and as a rule less common both in the lower sub-region (absent in the S) and in the Scandes. Typical species are *Salix myrtilloides*, *Ranunculus lapponicus*, *Carex tenuiflora*, *C. laxa*, *Eriophorum brachyantherum*, and (only in the N) *E. medium*, *E. russeolum*, *Polemonium acutiflorum*, and *Actaea erythrocarpa*. In their NE areas of distribution, *Saxifraga Hirculus* and *Stellaria crassifolia* belong to this group. *Pinguicula villosa* is common also on the E side of the Scandes. Rather similar is the area of *Parmelia obscurata* (AHLNER 1948 pp. 63—64, 111—112).

The upper limit of the middle sub-region, which on the whole

follows the foot of the Scandes, is difficult to characterize floristically. *Betula verrucosa* may be mentioned as a species that hardly reaches the upper sub-region, but it is rare also in some of the higher parts of the middle sub-region. Several true »Scandian» plants (species with us chiefly found in the Scandes) are found in the upper sub-region. *Athyrium alpestre*, *Carex rotundata* and *Pedicularis lapponica* are examples of such plants commonly descending into this sub-region. The forests become gradually more and more mixed with birch as we climb the mountain sides. In the S part of the Swedish Scandes, *Picea* is as a rule the predominating tree in this sub-region, with the exception of the northernmost part of Dalarna and adjacent parts of Härjedalen, where *Pinus* is almost solely prevailing. In N Lappland, *Picea* is almost or totally absent next to the mountains, and a belt of *Pinus* forest is intercalated between the mixed coniferous forests and the mountain birch belt. This *Pinus* belt was termed the »*regio subsilvatica*» by WAHLENBERG (1812 p. XXXII). The whole upper sub-region was termed »the subsilvine zone» by HEINTZE (1913 p. 15), the »*regio silvatica superior*» by DEGELIUS (1932 p. 7) and the »belt of mountain coniferous forest» by DU RIETZ. The forests of this region, the forester's »mountain forest», offer many troubles as to growth and reproduction. Besides the ordinary heath forest (often with a very thick humus layer) there are, esp. on irrigated soil, luxuriant meadow forests with tall herbs and grasses (e.g. *Lactuca alpina*, *Aconitum septentrionale*, *Geranium silvaticum*, *Rumex Acetosa* ssp. *lapponicus*, *Milium effusum*, ferns like *Athyrium alpestre*, *Matteuccia Struthiopteris*, and many others).

**The subalpine birch forest region.** Subalpine birch forest is very characteristic of the Scandes, but is known also from the northern Ural Mts. and from southernmost Greenland, and in the old times also from Iceland. The chief Scandian mountain birch (at least at higher levels) is *Betula tortuosa* Ledeb. The coniferous trees mostly occur scattered through the lower, and often also the upper parts of the subalpine region. This region has a moderate and very variable vertical extension (often less than 100 m but in the higher and western parts of the Swedish Scandes considerably more, up to 200—250 m).

If we disregard the birch and consider the lower layers of the vegetation, we shall probably find that the birch forest region is not a very natural one. There is only a gradual difference between its lower parts and the upper coniferous forest sub-region. Typical forest synusiae constitute the bulk of the under-vegetation, and true mountain plants



and communities play only a subordinate part. In the upper subalpine sub-region, on the other hand, the forest is split into scattered groups of birches, giving room between them to almost typical alpine communities with nearly the whole low alpine flora.

**The low alpine region** begins above the uppermost groves of birch forest. Single low birches and often also conifers (*Picea* in most parts of the Swedish Scandes) occur some distance further up. The reader is referred to the special literature for information about the alpine regions.

**The middle and high alpine regions** are almost entirely outside the scope of the present work. Mires do not occur in the high alpine region, and only small fragments of mire vegetation are found, sometimes, in the lowermost parts of the middle alpine region.

### How to carry out the regional study.

The best way to give a complete treatment of the mire vegetation of a large district is in my opinion to determine the plant communities present in different types of mire complexes, and to find out the regional differences by comparison, between equivalent communities within different complexes as well as between the mire complexes themselves. The construction of an elaborate »natural system» of the plant communities seems to be unnecessary and of limited value for this purpose.

However, it is at present impossible to carry out such a work in detail. The reason is that our knowledge is too fragmentary. Most investigations have been confined to very limited areas. Thus we have learnt much about these, but between them, there are large unknown district. A mire investigation map of North Sweden is not a map with large white patches, it is a white map with a few patches of investigated areas.

Considering the imperfection of our knowledge, as well as the incompleteness of the already existing summary synopses of the North Swedish mire vegetation (e.g. DU RIETZ 1933, 1942 b, 1949, OSVALD 1933, 1937, MALMSTRÖM 1942), I have made up my mind not to try to give a description of all the principal communities. As there is a considerable difference, both in the mire flora and in the external conditions, between various parts of the whole district under consideration, such a description cannot be given without due regard to the regional variation within each community, or group of related communities. Our knowledge does not permit such a treatment except in a few cases. In a previous work (1948 a, pp. 105—158, 284—286) I have

described the principal mire communities of the southernmost part of North Sweden (in the sense used here), with notes on their distribution and variation elsewhere (mainly in North Sweden). Much more cannot be done at present. I have, therefore, chosen another method, which is not new, but has hardly been tried in a treatise on vegetation, except in a popular account of the Swedish fen vegetation (lectures in 1949, to be published as SJÖRS 1950 b). The method rests on the concept of »direction of variation» (TUOMIKOSKI 1942) and implies, in short, that the whole material is examined with regard to these »directions». The material is then re-arranged for each »direction» taken under consideration. In my previous work (1948 a pp. 60—67, in Swedish; pp. 280—282, briefly in English) I have already given a short account of these »directions of variation». Only some slight alterations mainly concerning arrangement will be done now, but the subject will be treated more fully and with examples from different parts of N Sweden, esp. those studied in the field by myself. This is carried out in the following two sections. Because of the extreme conditions in the mosses (bogs), these and the fens are dealt with separately. Then follow two sections on the local and regional geographical differentiation of the mires.

The meaning of the special terms used was defined and discussed in SJÖRS 1948 a (pp. 38—67, in Swedish; pp. 279—282, briefly in English).

The history of the mires is not dealt with in the present work, nor are the successions taking place in the mire communities. A general tendency of the latter to become less hydrophilous in the present time is evident for instance in coastal Österbotten, Finland (BRANDT 1948) and on Gotland (PETTERSSON 1949), and may be traced at least in the less humid parts of N Sweden, too.

### **Moss or bog vegetation.**

Moss or bog vegetation occupies the ombrogenous parts of the mires, where mineral soil water is absent, or at least practically without influence. It plays a great rôle only in the S and SE parts of North Sweden, and in certain valleys in W Jämtland. Scattered examples of areas with continuous moss vegetation have been found in many different parts of Norrland, and there is little doubt that such vegetation occurs almost over the whole country, even if as a rule the necessary hydrographical conditions are but rarely fulfilled. Less extensive islands or isolated hummocks or banks of moss vegetation are widespread,

but they do not show the complete range of this series of vegetation, as only the drier stages are represented.

The moss vegetation shows only two really important kinds of »directions of variation». One is the series of wooded hummock — woodless hummock — lawn — carpet — mud-bottom communities, the other is the geographical differentiation. The former series, as it is represented in S Dalarna (and adjacent provinces) was fully described by SJÖRS 1948 a (pp. 107—116, 285, Tables A—E). Further N, there are some differences.

The wooded (pine-clad) mosses cover large areas only in the coastal provinces. GRANLUND (1932 pp. 28—31) determined their percentage ( $>20\%$  of the whole peat land area) in the districts near the *limes norrlandicus* and stated that »this both soligenous and ombrogenous wooded moss type continues as a transition along the whole limit of raised mosses as far as its northernmost point in S Västerbotten (cf., for example, SMITH 1918). In Jämtland, too, the few true raised mosses are wooded.» The true wooded moss is of course not soligenous, but may slope unilaterally like a soligenous fen, and often also occurs together with water tracks or wet »windows» of soligenous origin. The wooded mosses in the uplands are as a rule of this latter type. Those in Västerbotten have been described by MALMSTRÖM (1923 pp. 42, 50, esp. the *Ledum* type). They contain as a rule some scattered fen plants (e.g. *Carex globularis*, *C. pauciflora*) and gradually merge with the fen hummock communities. Further N, e.g. in Muddus National Park in Lule Lappmark, true wooded mosses are rare, similar fen hummock communities prevailing there. On the other hand, it is also difficult to distinguish these mosses from wet heath-forest on mineral soil. In the flat Central Muddus, the transitions are very gradual; the same plants, in the field layer mainly *Betula nana*, are the chief dominants in both, and the rest of the flora is also practically the same. There are, in both, scattered wet pits with some boulders at the bottom and with a scanty vegetation usually containing some fen species or other. These »boulder-pits» (»stengropar»; LUNDQVIST, e.g. 1948) are typical of the mire margins in this cold continental district, and are due to frost action. The tree layer contains both pine and spruce, but the latter tree probably needs some influence from the mineral ground underneath the very shallow peat.

*Ledum palustre*, an eastern species, mapped by GRANLUND (1925) and HULTÉN (1950), is an important dominant mainly in the coastal provinces. Where *Ledum* is absent or scarce, *Vaccinium uliginosum*,

*Betula nana* and *Calluna vulgaris* are as a rule the most common dominants of the field layer. The bottom layer, which is seldom well-developed, contains rather numerous lichens and heath bryophytes besides the *Sphagna*, of which *S. fuscum*, *S. nemoreum*, *S. magellanicum*, and *S. parvifolium* are the main dominants.

Moss hummock vegetation, transitional between open and wooded, (with scattered pines) is known from Jämtland (Kyrkås parish; SJÖRS 1949 a pp. 97, 100), Ångermanland (MELIN 1917), and Västerbotten (MALMSTRÖM 1923 pp. 43, 50).

Moss vegetation, as a rule with scattered trees, also forms the long hummock banks of the northern mixed mires. The chief field layer dominant is mostly *Betula nana*, and *Sphagna* are less prominent than lichens and heath mosses in the usually scanty bottom layer.

The woodless moss hummock vegetation is widespread all over N Sweden up to the low alpine region.

In and near the Scandes, the mosses are entirely treeless. This is also the case at least in some parts of Central Jämtland, contrary to the above statement quoted from GRANLUND (which does apply, strictly spoken, only to the true »raised», i.e. domed, mosses).

There are two main types of this vegetation: such as is rich in *Sphagnum fuscum* (or sometimes *S. nemoreum*) and such as is not. The latter type is very variable. Besides the wide-spread dominants among bryophytes and lichens (*Dicranum Bergeri*, *Pleurozium Schreberi*, *Polytrichum strictum*, *Mylia anomala*, *Cladonia alpestris*, *Cl. rangiferina*, and *Cl. silvatica*) there are many other interesting species of the bottom layer. *Rhacomitrium lanuginosum* is common in W Jämtland on the higher hummocks, which is a pronouncedly oceanic feature in their vegetation. *Webera sphagnicola* and small hepatics like *Calypogeia sphagnicola* are probably common over most of N Sweden. *Dicranum elongatum* grows in dense cushions esp. on the subalpine and low alpine moss hummocks. *Mylia Taylorii* occurs in mosses in W Jämtland and W Dalarna. I have found *Orthocaulis Binsteadii* in most mosses that have been well searched in the middle and upper coniferous forest subregions as well as in the Scandes. Among the lichens there is an interesting group, which the moss hummocks share with the mountain wind-heath, viz. *Cetraria nivalis*, *C. cucullata*, *Alectoria ochroleuca*, *Ochrolechia frigida*, and sometimes other species (cf. a future work by HASSELROT). In the W Jämtland mosses, the highest hummocks are often crowned with a vegetation that gets a whitish look from these and other lichens (e.g. *Cladonia* spp., *Icmadophila ericetorum*) together



with *Rhacomitrium lanuginosum*. No doubt, these hummocks have a very thin snow cover in winter. Sometimes vascular plants characteristic of the mountain heaths (e.g. *Loiseleuria procumbens*) are present, too. In the shallow parts of these mosses, there are often knolls of sand with similar vegetation constituting stations of the mountain vascular plants *Loiseleuria procumbens*, *Arctostaphylos alpina*, *Juncus trifidus*, *Carex Bigelowii*, and *Lycopodium alpinum*.

The field layer is usually dominated by *Calluna vulgaris*. In those parts of the Scandes, where *Calluna* is less common or absent (mainly in the N; see HULTÉN's map, 1950), *Empetrum hermaphroditum* replaces it. This northern species, or sometimes the southern *E. nigrum* (in Bergslagen and Jämtland), is frequently dominating on the wind-hummocks. *Rubus Chamaemorus* or *Betula nana* are often very conspicuous. The latter is the single dominant in a type of moss that is probably very shallow and has no hollows. Such a moss covers most of the Rödflo, a small mire 2 km SW of Fyrås, Hammerdal parish, Central Jämtland. It may be of importance that this moss rests on non-calcareous soil, as is evident from the vegetation round a small, shallow pool on its border (there is not a single calciphilous plant, although a pronouncedly calciphilous vegetation occurs only some hundreds of m from the Rödflo). Other examples are found in Muddus. — A type with *Andromeda Polifolia* as dominant was observed by MALMSTRÖM in Västerbotten (1923 pp. 43, 50). It was stated to be the poorest of all the mire communities but nevertheless presented a sparse tree layer of pines. Entirely treeless hummock communities were not found in the Degerö Stormyr complex, nor in MELIN's (1917) district of investigation.

Moss hummock vegetation from Bergslagen, the southernmost part of N Sweden, has been described by me (1948 a, p. 109 and Table B, 1949 c, 1950 a), from the mountains in Dalarna by SAMUELSSON (1917 pp. 215—216), from Jämtland by BOOBERG (1930 pp. 31—53, in part), DU RIETZ (1933), and me (1946 b, 1948 b, 1950 a), from Ångermanland and adjacent provinces by MELIN (1917 pp. 124—144), from Västerbotten by MALMSTRÖM (op. c.), from the forest land of Lule Lappmark by me (1946 a) and from the mountains there by BJÖRKMAN & DU RIETZ (1923), from Torne Lappmark by TH. C. E. FRIES (1913 pp. 143—147) and by DU RIETZ (1921 a, 1921 b p. 161, 1925 pp. 30—31, 1942 b).

The moss hollow vegetation has a much more restricted distribution in N Sweden. There are two reasons for this: the common soligenous water influence between the moss hummocks that tends to

replace the moss hollows with fen areas, and the shallowness and seasonal dryness of much moss-covered ground, that only allows the development of hummock vegetation. These questions will be discussed below (e.g. p. 207). Moss hollows have only developed in those mosses that are not too small and shallow and that at the same time are well sheltered from the influence of soligenous water. Such mosses are found in the S and coastal provinces and in the valleys of W Jämtland (but not in Central Jämtland, as far as I know), and as exceptional formations elsewhere. I have found four small mosses with hollows (representing as many different types!) in Muddus. Also some examples have been found on mountain terraces.

The hollow vegetation is composed of three very different-looking, though floristically not very well separated, plant communities. I have described (as associations) those in Bergslagen (1948 a pp. 110—116, Tables C—E). DU RIETZ (1949 pp. 285, 301) maintains a somewhat different opinion regarding the associations of S Swedish moss hollows. My three associations are analogous to the »lawns», »carpets» and »mud-bottoms» in the fens and may be termed in the same way, although the word »lawn» hardly suits these thin and tussocky *Scirpus caespitosus* and *Eriophorum vaginatum* communities. Chiefly the latter species is also found in the carpets and mud-bottoms. In the carpets, it shares the dominance with, or is subordinate to, one or more of the following species: *Scheuchzeria palustris*, *Carex limosa*, and *Rhynchospora alba*. The latter (which is sometimes, esp. in S Sweden, found in lawns), occurs in N Sweden almost exclusively in the lower coniferous forest sub-region, and *Scheuchzeria* is absent in certain (but not all) mosses in or near the Scandes. These species prefer a loose, more or less quaking peat-ground, whereas the lawn vegetation is more firm. The *Sphagna* are only partly different: *S. balticum*, *S. tenellum*, and *S. compactum* prefer lawns, *S. cuspidatum* (not known from the N districts), *S. Dusenii*, and *S. Lindbergii* prefer carpets. The distribution and ecology of the latter northern species have been recently dealt with by me (1949 b). The mud-bottoms resemble the carpets as to field layer (sometimes totally absent) but have no continuous bottom layer of *Sphagna*. These are replaced by luxuriant algae (at least in Bergslagen, mainly the purple *Zygogonium ericetorum*) growing on the bare peat or mud surface, which is submerged in wet periods. Transitions between lawns and mud-bottoms are common. The lawn vegetation then forms isolated tussocks separated by a mud-bottom network.

The various kinds of hollow vegetation are not equally distributed. Lawn hollows occur over the whole area, but only where the supply of water is not very great. Carpets are most common in the mosses along the *limes norrlandicus*. In the colder and more humid climate of the W and N, they are to a certain extent replaced by mud-bottoms. In the mire Navarkölen, of Malung and Äppelbo parishes in Dalarna (SJÖRS 1948 a p. 226, Pl. 11 B) and in many mosses in W Jämtland, the mud-bottom hollows have very large dimensions, taking up most of the moss surfaces. The parts of the mosses with mud-bottom hollows have a considerable flow of water and are more or less erosive. In the W Jämtland mosses, the erosion often leads to the formation of brooks which drain the moss, stop the growing of the peat and may ultimately break down large parts of the mosses.

Ancient mud-bottom hollows which have not been drained may develop into water-filled pools as the peat grows thicker. Whole hollow-pool complexes occur in many mosses in the S (SJÖRS 1948 a pp. 186—227, with map p. 269; in addition may be mentioned a few mosses near the coast, e.g. one in Hamrånge parish, Gästrikland, SMITH 1918 pp. 292, 325). They are also found in W Jämtland mosses. Three considerable pool complexes occur in the remarkable moss on the peninsula of Halsen projecting into Lake Ånn. I have also found hollow-pools in a moss near Åkroken in the upper Långan valley (Kall parish; SJÖRS 1946 b p. 23), and a single hollow-pool was observed in a moss at Saxvallen (Åre parish) during an excursion of DU RIETZ'. Mud-bottom hollows with shallow but probably permanent water are more common.

The geographical variation within the mosses has already been spoken of above in various connections, concerning both floristical variation mainly caused by unequal distribution or ecological demands of certain species, and variation regarding the distribution of the plant communities.

The mosses form one end point of the series moss — poor fen — rich fen. All communities of mosses occupy almost the same position, viz. the terminal one, in this series, the whole rest of which is composed by fens. Strictly speaking the mosses and the fens are units of different orders, like the end link contradistinguished from the rest of a chain. There are some facts that support such an unequal division. In many mire complexes the mosses equal or exceed the fens in area. In many cases, esp. S and E of the zone with soligenous »wet of soil», there is an obvious gap in the series. Where mosses are in close connection with soligenous poor fens, the mosses are often more difficult to distinguish from the fens, because transitions exist

and may even occupy wide areas. Thus, for instance, *Carex pauciflora* may grow in a vegetation that in almost all other respects seems to be typical moss.

### Directions of variation within the fen vegetation.

As the fen vegetation represents a much greater »variation range» than the moss vegetation, many more directions of variation can be distinguished within it. This is the main cause of the discordance between the various attempts to treat its variation in the form of vegetation systems. Almost every author writing on fen vegetation has proposed his own system (or systems!), different bases of subdivision or classification (corresponding to directions of variation) being applied in varying order. On the other hand it is not easy to determine all these directions, as they are often complicated or dependent of each other. The following account must be regarded as preliminary.

### Variation due to unequal geographical distribution of species.

Many examples of unequal distribution of fen species have already been mentioned in the section on the vegetation regions of N Sweden. There is, in addition, a group of southern calciphilous species, which are rare or absent in most parts of the lower coniferous forest sub-region but occur in the Cambro-Silurian districts on Lake Siljan and in Jämtland. *Schoenus ferrugineus*, *Carex lepidocarpa* s. str., *C. Hostiana*, and *Ophrys insectifera* are typical examples among the fen plants (most species of this group prefer mineral soils).

The poorest fen flora is found in the NE (Central N Lapland and N Norrbotten). In spite of a surprisingly wide extension of rich or at least intermediate fens, this country is pronouncedly non-calcareous, and offers only few and widely separated, possible stations for a true calciphilous flora. But at the same time numerous oligotrophic as well as somewhat more exacting species of a weakly southern type of distribution are absent or rare. *Carex echinata*, *C. fusca*, *Phragmites communis* and possibly also *Potentilla erecta* may be mentioned. Only two fen species, *Eriophorum medium* and *E. russeolum*, are confined to this district.

There are also a few species that show the contrast between the W and the E. *Narthecium ossifragum* occurs in abundance in the sloping fens of westernmost Jämtland. Among the bryophytes there are additional western fen plants, e.g. *Sphagnum auriculatum*, *S. imbr-*



*catum*, both of which also occur in the S and SW, together with *S. molle* (SJÖRS 1949 a p. 98). The less pronouncedly western *S. pulchrum* is common at least in the uplands of Bergslagen and W Dalarna and in W Jämtland, and has been found in several other places, esp. in Ångermanland, as far N as Lycksele Lappmark (cf. SJÖRS 1948 a p. 130).

Of plants which have an eastern distribution in N Sweden and which at least sometimes may be found in fens, *Ledum* has already been mentioned. *Rubus arcticus* is less eastern; it is rare in the S parts. *Carex globularis* is very common over most of N Sweden (even the SW parts) but is absent or rare in W Jämtland and W and N Lappland (HULTÉN's map). *Sphagnum Wulfianum* is a less common but widely distributed eastern species. (Regarding European distribution, all these species are north-eastern rather than eastern). *Chamaedaphne calyculata* is our most extremely eastern mire species. It grows in about the same habitats as *Ledum* (moss and fen hummocks esp. wooded, etc.) and is only found in Norrbotten.

The subalpine and alpine fens, and also those of the upper coniferous forest sub-region, often contain a few »Scandian» (see p. 177) fen plants. It is remarkable that only one of these is oligotrophic, viz. *Carex rotundata* (a species that is sometimes found in the N part of the middle coniferous forest sub-region, too, e.g. in Muddus, where it is not common). *Eriophorum Scheuchzeri* may be added, but it is so widespread in the coniferous forest region that it is dubious whether it should be called a true Scandian plant. The bulk of the Scandian fen plants are calciphilous even if not always restricted to calcareous fens. Typical more or less widespread species are, e.g., *Carex atrofusca*, *C. microglochin*, *C. saxatilis*, *C. adelostoma*, *Saxifraga aizoides*. To the southern group of distribution belong *Pedicularis Oederi* and *Kobresia simpliciuscula*, both of which often grow in fens, to the bicentric group in a broad sense *Juncus castaneus*, *Carex parallela*, and to this and the northern group a few other species that may occur in fen-like communities. — It must be strongly emphasized that many, if not most, of the calciphilous fen plants typical of the Scandes are not Scandian plants (or mountain plants) in a restricted sense, because they occur commonly in fens not only in the upper, but also in the middle, and in a few cases even in the lower coniferous forest sub-regions. As stated above, they are especially common in the fens of Central Jämtland.

From the above it is evident that a general division of the N Swedish fens into one »subformation of the Scandes» and one »subformation of the

North Swedish coniferous region» (preliminarily proposed by DU RIETZ 1949 pp. 287, 301) is not very well founded from a floristical point of view, and that this is especially the case with regard to the oligotrophic poor fens. The subalpine and alpine fens, which according to DU RIETZ constitute the former »subformation», are hardly so »easily recognized through the absence of many southern fen plants as well as the presence of numerous mountain plants» as he declares. The disappearing of the southern plants as we proceed towards the N and the mountains is a much more complicated matter, the descending of the northern and the Scandian plants likewise. Moreover, the lower part of the subalpine region and the upper coniferous forest sub-region are often very similar with respect to the fens. Pronounced changes take place within the subalpine region and within the coniferous forest region, too.

The greatest regional floristic difference is found in the calcareous fens, the extreme rich fens or the suballiance *Euscorpicion* of DU RIETZ (op. c. pp. 296, 297, 303—304). NORDHAGEN (1943) distinguished between the *Cari-cion atrofuscae - saxatilis* of the Scandes and the *Schoenion ferruginei* in the lowland. The former was accepted by DU RIETZ as the representative of the *Euscorpicion* in the Scandes. The extreme rich fens of the Jämtland Cambro-Silurian are, as DU RIETZ remarks (pp. 296, 304), composed of several very different but as yet not sufficiently investigated types. The intermingling of southern and northern and sometimes even more or less Scandian species is a striking feature of these fens, the largest of their kind in Fennoscandia. The extreme rich fens of Dalarna are intermediate between those of Jämtland and of S Sweden, and those of N Uppland, Östergötland, Västergötland and Gotland still possess some northern species. As a matter of fact, we have an almost continuous series of connecting links between the Scanian, Ölandian and Gotlandian extreme rich fens with their strong component of southern species, and those of the Scandes with their typical Scandian and northern flora.

### The poor fen — rich fen series.

My studies in this direction of variation are to be published in another paper (1950 c). The direction is of very great importance, but in my opinion not the only one worthy of consideration as a primary direction of variation. Most authors have divided the fens into two main parts, using this direction as a basis. Thus, DU RIETZ (e.g. 1942 a and b, 1948, 1949), WALDHEIM & WEIMARCK (1943), WALDHEIM (1944), V. KRUSENSTJERNA (1945), and others, have distinguished the »poor fens» and the »rich fens», and have also proposed a further subdivision of these according to the same direction. The range is so great that the parts established through such a division are not homogeneous with respect to this direction of variation itself. Esp. in North Swedish fens the variation is often found to be quite gradual. Thus, for instance, fens more or less intermediate between »poor» and »rich» are extensive in North Sweden.

This direction of variation is connected with the chemical composition of the fen peat and water, esp. the degree of »neutralization» or »saturation with bases» of the acid components in the mostly high-molecular peat substances. The pH, the electrical conductance, the concentration of metal cations in solution, the total amount of bases in the peat, and other measurable quantities give some information of this complex of chemical conditions, but do not indicate or constitute the factors as they affect the plants (SJÖRS 1948 a pp. 101, 246—247, 249—251, 287—288). Thus, a direct coincidence between the vegetation and any of these chemical conditions cannot be expected, nor, as a matter of fact, is it to be found. The nature of the correlation that is really found is briefly discussed in the paper mentioned above (1950 c).

### The mire expanse — mire margin — spring fen direction of variation.

There is an appreciable difference regarding both flora and vegetation between the open expanses and the marginal parts of the fens. In mosses, the distinction between the central open area and the marginal forest is analogous only in part, because both are independent of the chemical influence from the mineral soil and thus the vicinity of the latter cannot play such a direct rôle as is possible in the fens. Nevertheless the wooded moss hummock communities have a striking affinity with the fen margin communities, mainly in connection with the fact that the latter generally have a tree layer, too.

Mainly as a result of a cartographical analysis of the distribution of the majority of species within a special area (SJÖRS 1948 a, the »Small Maps»), I was able to show that the direction of variation of fen expanses as contrasted with fen margins is really an important one in the composition of the vegetation. Of course, this variation had been noticed before. For instance, CAJANDER's (1913) *Bruchmoore* are a group of fen margin communities, and the same is mainly the case with NORDHAGEN's (1936, 1943) *Caricion canescentis - Goodenowii*. DU RIETZ spoke of »poor fens adjacent to the mineral soil» in 1940 (mentioned in his work of 1949, p. 293). The contrast between mire margins and mire expanses in the fens was stressed by him (1948 pp. 72, 77), and these terms were adopted. — Of course, the position of a certain fen community in this series of variation is determined from its composition, not from its location in relation to the mineral soil.

Some of the important species characteristic of the mire expanses have been listed in SJÖRS 1948 a p. 65 (*Scirpus caespitosus*,

*Carex limosa*, *C. livida* etc.). The list was composed without regard to other directions of variation; thus species of poor fens were listed together with species of rich fens, e.g. *Schoenus ferrugineus*. (In S Sweden, for instance on Gotland, *Schoenus ferrugineus* grows in spring fens and also in open marginal parts of the fens; PETTERSSON 1946 p. 180, 1950.) Many species seem to be more or less closely restricted to the mire expanses (e.g. the mentioned species, *Rhynchospora alba*, *Juncus stygius*, *Eriophorum medium* in the NE); other plants, e.g. *Scheuchzeria* and many mosses, prefer the mire expanses but are by far not confined to them. Many species are practically indifferent to this direction of variation, among which are such important dominants as *Betula nana*, *Myrica Gale*, *Carex rostrata*, *C. lasiocarpa*, *C. chordorrhiza*, *Eriophorum vaginatum*, *E. angustifolium*, *Molinia coerulea*, and *Menyanthes trifoliata*. Then we pass to species more or less preferring the fen margin communities although not absent in expanse vegetation: the trees (*Picea Abies*, *Betula pubescens*; less clearly also *Pinus silvestris*), *Juniperus communis*, *Vaccinium Myrtillus*, *V. Vitis-idaea* (less clearly *V. uliginosum*), *Potentilla palustris*, *Carex magellanica*, *C. echinata*, *Orchis maculata*, *Sphagnum parvifolium*, etc. (op. c. p. 65 below). Somewhat more strongly preferring the margin vegetation are, e.g., *Salix lapponum*, *Carex fusca*, *C. canescens*, *Calamagrostis purpurea*. Mostly confined to it are, for example, *Equisetum silvaticum*, *Corallorhiza trifida*, *Carex vaginata*, *Maianthemum bifolium*, and still more strongly *Salix aurita*, *Carex globularis*, *Juncus filiformis*, as well as many species normally growing on mineral soil but sometimes present in fen margins in the immediate vicinity of the mineral soil.

It is evident that the distinction between expanse and margin fen communities is a gradual one and that a sharp boundary is not present if we regard the bulk of the fen communities. DU RIETZ denies (1949 p. 290) that such a boundary should be «of as high a rank as the boundary between poor fen and rich fen, neither with regard to the sharpness of the boundary nor to the magnitude of the differences between the vegetation units separated by the boundary». There is not, in either respect, a question of sharp boundaries, but a gradual passing from one extreme to the other, through a continuous series of variation (which may, of course, be incomplete in many actual cases in the field, causing an abrupt difference or distinct boundary to appear). Which difference between the extremes that is considered the larger one is chiefly of interest if we aim at the construction of a branched system; as a matter of fact both are as large as to warrant a treatment as fundamental directions of variation.



The expanse and margin fen communities of Bergslagen (mainly the Skattlösbergs Stormosse) have been dealt with in SJÖRS 1948 a (pp. 116—153 and Tables F—T). In other districts, the margin communities are less well-known. A striking feature is the very large extension in the NE of wooded margin fens, of which especially the hummock fen communities that are very poor in species are important. They are often very similar to moss hummock vegetation but differ in the presence of *Carex globularis*, *C. pauciflora*, *Equisetum silvaticum*, or some other fen plants (SJÖRS 1946 a pp. 87, 88; regarding the *Carex globularis* vegetation see SJÖRS 1948 a pp. 140—143 and the literature cited there; cf. also below, p. 195). In the western, more humid districts, esp. at a higher altitude, the fen margin communities often become less extensive relatively to the fen expanses and are often woodless; they also differ in other respects.

The habitat conditions constituting the background of this direction are little known, and probably of a complex nature.

The special character of the vegetation in springs has long been noticed. This vegetation has a great affinity to that of the mire margins, being in many respects more marked than the latter, and has also qualities of its own. There are several directions of variation within it, esp. that of strong springs as contrasted with spots with slowly out-trickling water, that of the central parts as contrasted with the peripheral, that of spring fen as contrasted with spring meadow, and that of transitional poor fen (*Sphagnum riparium* springs), intermediate fen (e.g. *Scapania uliginosa* springs), transitional rich fen (e.g. *Webera albicans* v. *glacialis* springs, mainly in the Scandes), and extreme rich fen (*Cratoneurum* springs); see below, p. 200. The ecology of N Swedish spring vegetation is discussed in SJÖRS 1948 a (pp. 66, 153—158, Tables U, V), and the chief literature listed (in addition WITTING 1949 pp. 727—728, 734, 735; SJÖRS 1950 a pp. 29—31, 34—35).

### Tree growth in the fens.

The direction of variation concerning tree growth is not an independent one. The growth of trees is correlated with the mire margin conditions, and as a rule also with a certain dryness of the soil. But trees are not found in all mire margin communities, nor on all comparatively dry soils in the mires. A special discussion of the growth of trees seems warranted.

Our Swedish trees lack an organization for rooting in soil con-

stantly free from oxygen, and there seems to be little doubt that trees are confined to the parts of the mires where, at least at intervals, some oxygen is present in the uppermost layers of the soil. This can be accomplished in several ways. The water-table may be low, or more correctly, may have low minima in summer periods of drought, so that air replaces the water in cavities near the surface. But as the peat contains oxygen-consuming compounds, the process must be frequent and the access of the air easy in order to result in possibilities for tree growth. Cf. ROMELL 1922. Tree seedlings are often found in all sorts of mire communities, even very wet ones, but for a further development the amount of aerated surface peat seems in most cases to be insufficient.

The best conditions for the trees are found on hummocks. But the ordinary moss (bog) or moss-like hummocks support as a rule only dwarfed and scattered specimens, mostly pines. The true wooded fens have a special type of »tree-hummocks» (SJÖRS 1948 a pp. 64, 143, 147, 149—150, 263). TUOMIKOSKI (1942 pp. 20—25) has pointed out that there is invariably a kernel formed by an old stump or by the base of a living tree in the centre of these tree-hummocks. Thus the possibility of tree growth is strongly promoted by former tree growth, and the process is one of several tree generations. In the case of *Alnus glutinosa*, present almost only in the lower coniferous forest sub-region of N Sweden and uncommon except in the S and SE, the tree hummocks are very conspicuous, and new stems are constantly developed from stump shoots. *A. incana* and *Betula pubescens* grow in the same way, although the tree-hummocks are lower and more overgrown with less specialized bryophyte communities. The former species also multiplies by root-shoots, but is of less importance as a fen plant, being probably too demanding with respect to oxygen in the soil. The coniferous trees, which of course multiply by seedlings, are also dwellers of the tree-hummocks, being favoured as young plants by the decaying wood in the centre (cf. SERNANDER 1936, ARNBORG 1942, etc.).

On wet soil with moving water, tree vegetation sometimes occurs, too. It seems probable that this is also due to oxygen in the soil, but in this case dissolved in the ground water. Real wood is mainly confined to shallow peaty soil, especially along brooks. Along larger brooks where the soil is waterlogged and even submerged in springtime, a very beautiful light birch wood often fringes the banks, usually with a shrub layer of willows.

The chief fen trees in N Sweden are *Picea Abies* and *Betula pubes-*

*cens. Pinus silvestris* is usually present, and is predominating in very poor fen margin vegetation resembling the mosses (bogs).

The growth of trees in the mires displays a markedly eastern tendency common to both the fens and the mosses. The »*Bruchmoore*» of the CAJANDER (1913, etc.) school in Finland (cf. TUOMIKOSKI 1942 p. 23) are eastern, and their importance in Sweden is by no means so great as in Finland. Very rich wooded fens in SE Gästrikland have been described by SMITH (1919 pp. 219—222) and in Central Jämtland by BOOBERG (1930 pp. 106—112), and less rich types are commonly distributed in the coastal and continental parts of N Sweden. In the less continental, more humid SW and W parts, the wooded fens are subordinate, and almost quite absent in the suboceanic W Jämtland upper coniferous forest sub-region. In the subalpine region, a tree layer of birches seems to be developed only in some willow-dominated fens of a rich, meadow-like type.

#### Presence of a shrub layer.

Shrubs in N Swedish fens are above all willows. Other shrubs and shrub-like ligneous plants are young birches, the hybrids between birch and dwarf-birch, *Juniperus communis* and *Rhamnus Frangula*; the latter two belong to rich fens, although the juniper is much more common and may be found in fen margins of a less rich type. *Rhamnus* occurs mainly in the lower coniferous forest sub-region.

Among the willows, the grey-leaved species *Salix lapponum* and *S. glauca* are prevailing, esp. in the north (the latter species is rare in the lower coniferous forest sub-region). *S. phylicifolia* sens. lat., *S. aurita* (chiefly in the lower sub-region), and several quantitatively less important species occur in the fens, too.

The typical willow-fens are found in several different situations. One is the area of regular springtime inundation along the shores of mire lakes and slowly-running streams (in the latter case, a tree layer mainly of birches is often developed). These willow scrubs are dense but moderately high (1 to 2 m). Irrigated banks and deltas of quicker mountain streams may carry a still more tall and dense willow vegetation (often on mineral soil), but perhaps the most imposing willow thickets are those of spring soil. They may reach several metres in height and may be almost impenetrable. Less dense are the common willow scrubs of the mire margins, and those of the wet mountain-sides in the Scandes. Although most of the willow species ascend higher,

typical thickets are mainly confined to the lowermost part of the low alpine belt. The maximum of the willow scrubs is located in the sub-alpine region, especially in sheltered valleys. They are also very significant and common in the upper and middle coniferous forest sub-regions.

Although there is a rich literature on the willow scrubs (listed in part in SJÖRS 1948 a p. 151; in addition SJÖRS 1950 a p. 34, SELANDER 1950), their ecology is little known. It seems probable that they are favoured by oxygen in the subsoil water, that a moving condition of the latter is preferred, and that a strongly acid reaction and extreme poor fen conditions are always avoided. In a Muddus mire of the ordinary type, the roots of the water tracks may easily be located by means of the willow thickets: absence of willows in the mire margin means moss- or bog-like poor fen vegetation without strong irrigation, at least not from other than very superficial and acid layers of the mineral soil. — As to the under-vegetation, it has thus the character of transitional poor fen or rich fen, and is always of the spring fen or fen margin type, practically never containing the typical mire expanse plants.

#### Variation according to wetness.

The height of the water-table was used as a primary basis of subdivision of the mires already by WEBER (1902 p. 227) who distinguished between aquatic, helmatic, semiterrestrial, and terrestrial mire vegetation. No doubt, this classification is corroborated by a direction in the variation of the vegetation itself. LUMIALA (1944) made measurements of the height of the ground water table in different communities of quaking mires, where this level is reasonably constant relatively to the mire surface and to the plants. But such measurements cannot give an idea of the conditions in the majority of mire communities which grow on soil with strongly changing water level. I have shown that these changes are of very different magnitude in different parts of the same mire (1948 a pp. 39–42, 86–94, 279, 283–284). Thus, the relations of the plants to the water level are by no means of a simple nature. This has been even more strongly emphasized by KULCZYŃSKI (1949), who regards the changes in height of the relative water level as a primary cause of the development of several different kinds of mires.

Nevertheless, there are obvious relations between the ordinary water conditions of the habitat and the vegetation. The extremes, the



always submerged aquatic vegetation and the never submerged terrestrial vegetation, are easy to characterize from the plants, but the intermediates display less regular conditions. Only with respect to most of the bryophytes can we speak of true indicator plants of the water level as such. They are indicative of the conditions at moderate to good, but of course not maximal, water supply. The conditions at extreme drought are of minor importance to the bryophytes, because they all seem to be capable of standing occasional but complete drying up of the habitat, such as took place in 1945 in the N part and in 1947 in the S part of N Sweden.

According to DU RIETZ, the variation in the wetness direction displays itself in the poor fens through the differentiation into the associations *Rostrateto - Apiculatetum*, *Vaginateto - Papillosetum*, *Polytrichetum* (1949 p. 294), and *Fuscetum* (p. 297). In the rich fens, the associations are (1933, 1949 p. 287) *Scorpidietum*, *Drepanocladetum*, *Campylietum*, *Tomenthypnetum*, and *Fuscetum*. This differentiation was first made clear by BOOBERG (1930). Unions of the bottom layer only slightly differing from the bottom layers of these associations have been mentioned by WALDHEIM (1944) and V. KRUSEN-STJERNA (1945).

In »certain North Swedish transitional rich fens» DU RIETZ (l.c.) has found the associations *Loeskypnetum* and *Subfulvetum* above the *Scorpidietum*; citing the incomplete description of these new associations in WITTING 1949 (pp. 721—723). There are many examples of this kind of vegetation in the earlier literature (e.g. CAJANDER 1913 p. 117, MELIN 1917 pp. 72—74, 77—86, 112—115 [in part], NORDHAGEN 1928 pp. 459—462, 1943 p. 480, SJÖRS 1943 p. 84, 1945 p. 425, 1946 a p. 92, 1946 b pp. 41—46, 1948 a pp. 122—125, Tables I nos. 11—25, J nos. 6—21). The association growing below the two mentioned above (which are not very well separated from each other) is often not *Scorpidietum* but a poorer »*Calliergonetum sarmentosi*» (the name is new) without *Scorpidium scorpioides*, *Calliergon trifarium*, *Cinclidium stygium*, *Drepanocladus intermedius*, and other more advanced rich fen bryophytes, but with the *Drepanocladus* species *purpurascens*, *procerus*, or *revolvens*. Examples: MELIN 1917 p. 54 nos. 1—4, p. 56 nos. 1—7, SAMUELSSON 1917 p. 204 (spring fen variant), some of the analyses in NORDHAGEN 1928 pp. 390—398, KALLIOLA 1939 p. 80—84, 480—491, SJÖRS 1946 b pp. 68, 80 (spring fen variant), 1948 a pp. 131—133, Table N nos. 1—27, 56—58, WITTING 1949 p. 736 nos. 49 and 48. For autecology of the chief bryophytes see ARNELL & JENSEN 1910, TUOMIKOSKI 1949, ALBERTSON 1949. The association (or the corresponding bottom layer union) is widely distributed in N Sweden, for instance in Muddus and in the Scandes, chiefly in non-calcareous districts. — Not seldom certain *Sphagna* are intermingled in this series of communities (e.g. *Dusenii*, *Jensenii*, *auriculatum*, *platyphyllum*, *pulchrum*, *subsecundum*, and *papillosum*, the latter mentioned by DU RIETZ); they make these communities pass without a well definable border line into the poor fens, and as stated in previous works (1945, 1946 a and b, 1948 a) and formally proposed in a contemporary one (1950 c), I prefer to treat these communities as intermediate.

The hummock — lawn — magnocaricetum — carpet — mud-bottom series.

The extreme »dry» end of this series is the same as that of the preceding one, and both series have a common »wet» end in the shape of true aquatic communities. But in the middle stages this series is different, as it does not indicate the water level as such, but properties of the habitat such as the firmness and aeration of the soil, which are more or less dependent on the water level and especially on its changes. Moreover, this series is not a simple one, but involves several interwoven directions of variation, too dependent on each other to be distinguishable as isolated directions. The consequence is that it cannot be regarded as linear, and that there are transitions between all the categories, and not only between those that are most strongly related to each other. In the last mentioned series the bottom layer plants were the best indicators; in this (complex) series the best indicators are those of the field layer, but the bottom layer has also a great importance.

The groups of this series were described in SJÖRS 1948 a (pp. 62—64, 281—282). I have found it necessary to add the group magnocariceta. With exception of the latter, these groups have their counterparts in the mosses, as stated above, pp. 180—184.

The fen hummocks are very similar to the moss or bog hummocks and connected with them by transitions. The fact that a hummock is surrounded by and developed from a fen is not decisive, but only the presence of fen plants. These are in the main vascular plants rooted in deeper peat strata of the hummock or below it. Some of them are survivors of the former lawn or carpet stage (e.g. *Molinia*, *Menyanthes*, and many others). More at home in the hummock vegetation are such fen species as *Carex dioeca*, *C. pauciflora*, *Equisetum silvaticum*, and in very poor fen margins there grows over most of N Sweden an almost »characteristic» species of fen hummock, viz. the eastern *Carex globularis* (cf. above, p. 190). The other species are the same as in the mosses: *Calluna*, *Betula nana*, *Rubus Chamaemorus*, etc. As most fen hummock communities have a tree layer (mainly of *Pinus*), the affinity is greatest with the wooded moss hummocks.

In the N and in the Scandes this kind of vegetation often lacks a tree layer. For instance in Muddus, it occurs both with trees and without, the latter kind having the character of a mire expanse community. Continuous areas of fen hummock vegetation are common in the drier parts of the mires, which are usually adjacent to mineral soil. There are three kinds of poor fen hummock communities in this vegetation,

viz., according as the influence of mineral soil water increases, a community with scattered *Carex pauciflora* as the only fen indicator plant, a community with *Equisetum silvaticum* in addition, and communities with willows (mostly *Salix lapponum*), *Calamagrostis purpurea*, and other plants of less poor vegetation able to penetrate the thin superficial layer of hummock peat. The fen hummock vegetation is usually provided with »windows» of wetter fen, or with the »boulder-pits» already mentioned (p. 180).

The hummock vegetation in fens has recently been discussed by DU RIETZ (1949 pp. 298, 304).

Through various transitions the fen hummocks are connected with the »lawns», or firm grassland fens (Sw. *fastmatta*; SJÖRS ll.cc.; 1950 a p. 14, 1950 b). These are, in the most typical cases, (i.e. those dominated by *Molinia coerulea* and *Scirpus caespitosus*), almost smooth and firm, giving a steady support to the foot. Often they are less lawn-like, the surface being more or less tussocky with tufts of *Scirpus caespitosus*, *Eriophorum vaginatum* (chiefly in poor fens) or *Schoenus ferrugineus* (in extreme rich fens). Numerous other species are found in lawns, and many of these are more or less preferential, both among vascular plants and bryophytes. Cf. Table 1 below and SJÖRS ll.cc.

The fen lawns are distributed all over N Sweden. Those of Bergslagen have been fully described in SJÖRS 1948 a (pp. 116—128, Tables F—L); less typical are the lawns of the mire margins (pp. 143—149, Tables Q, R). The W Jämtland lawns have been described by me (1946 b pp. 27—53, 90—91, an additional example in SJÖRS 1950 a p. 23) and earlier by HENNING (1895); from the Norwegian side of Mts. Sylarna NORDHAGEN (1928 pp. 407—426, 447—464) has given ample descriptions. We find typical lawns also in Central Jämtland, e.g. some extreme rich fen lawns of very different types. The *Schoenus* lawns of some mire expanses are tussocky, and very slightly sloping. On irrigated slopes there are sometimes smooth, firm lawns, with thin, highly humified and strongly calcareous peat. Some sloping lawns of the latter kind with a very rich flora are situated near Fyrås, Hammerdal parish, Central Jämtland. A short description in SJÖRS 1950 a (p. 30). These lawns are watered by small springs with out-trickling water. A similar example is given in SJÖRS 1949 a (p. 101); still richer are the Odensala spring fens near Östersund (DU RIETZ 1933 p. 67—68, LANGE 1938, WITTING 1949 pp. 727—728), but these include also carpets and mud-bottoms.

Lawns less rich in species, of types very similar to those in Bergs-

lagen, were described by MELIN (1917) from Ångermanland and adjacent provinces. In Degerö Stormyr (MALMSTRÖM 1923) only the poorest types of fen lawns were represented, but these had a large extent. Similar very poor *Scirpus caespitosus* lawns without *Molinia* and many other common fen plants, but with scattered occurrence of *Carex pauciflora*, are also found in Muddus. But here the somewhat richer lawns predominate, being common and extensive components of the mire pattern, especially in the sloping fens of the hilly parts of the area. The Muddus lawns are often more mixed with sedges, esp. *Carex lasiocarpa*, than is usual in the other districts investigated, and thus constitute transitions to the following group of communities.

Fen lawns are characteristic of humid conditions (SJÖRS 1948 a pp. 257—258, 288), and this is especially the case with poor fen lawns. They are chiefly localized to the sloping fens found in all humid parts of the area of investigation but are most well-developed and prevailing in the landscape in the subalpine and upper coniferous forest belts of W Jämtland, where the annual precipitation often exceeds 1 m.

We have now spoken of the part of the series growing on comparatively firm peat soil. The other fen communities grow on peat soil which is less firm and very wet under normal weather conditions.

The *magnocariceta* are dominated by tall sedges or other tall fen graminids. In this connexion, *Equisetum fluviatile* is regarded as a graminid, cf. SJÖRS 1948 a p. 163. This group of communities was not fully recognized in my previous work (1948 a), in part because such vegetation does not play a very important part in the Bergslagen mires and is moreover mainly represented there by transitions towards lawns, carpets, and mud-bottoms, to which groups, respectively, it was referred in the work mentioned. However, the typical *magnocariceta*, for instance those in SE Sweden (Uppland, Gotland etc.), deserve well the rank of a special group, to which also the generally less typical N Swedish examples may be conveniently referred.

In North Sweden many of the tall *Cyperaceae* are lacking, for instance *Cladium Mariscus* (limit in SE Gästrikland), *Carex paniculata*, and *C. riparia*. *C. pseudocyperus* and *C. elata* are confined to the southernmost parts (the former very rare). *C. gracilis* is common along the lower watercourses but is not a true fen species; towards the N and the higher levels it is more and more replaced by *C. aquatilis*, which forms, perhaps, the most typical *magnocariceta* in N Sweden. Occasionally, a dense tall growth is made up in the fens by several other species, e.g. *Phragmites communis*, *Calamagrostis purpurea* (often



in springs), *Carex vesicaria*, *Eriophorum angustifolium*, *Equisetum fluviatile*. The herbs *Menyanthes trifoliata*, *Potentilla palustris*, and *Lysimachia thyrsiflora* are often prominent in magnocariceta. But as components of these all other species are subordinate to the two common sedges *Carex rostrata* and *C. lasiocarpa*. These are, however, found in most other kinds of fen, and only the dense stands may be regarded as true magnocariceta.

A different type of magnocaricetum is that formed by tall tussock-forming species, esp. *C. juncella* and in some regions *C. caespitosa*. The very big tussocks of *C. juncella* grow along the mire brooks, separated by a network of wet mud-bottom, a type of land that is very difficult to penetrate especially when there are low, scrubby spruce and birch woods in addition to willow thickets.

The magnocariceta proper are dependent on very good irrigation and are as a rule submerged in springtime. Because of this and of the dense growth and strong litter formation of the field layer, the bottom layer is often poorly developed. The magnocariceta may be poor or rich fen. The chief dominants are common to both, because of which there is often little difference superficially. We find these communities along the shores of small tarns, lakes and brooks, and in areas that are flooded at high water or by brooks or springs. They constitute the best of the fens that were formerly, or still are, cut for hay in the regions where fodder is scarce; in old times this mowing was extended to large areas of sedge, grass, or horsetail fen. Even lawns, mud-bottoms etc. were mowed. The harvest was poor, hardly repaying the hard work. The chief phytosociological result of the mowing was that the willows were kept back. Sometimes the areas of mowing-fen were enlarged and improved by damming.

The magnocariceta lead over to true aquatic communities. A direct succession from these to fens takes place in the sheltered bays of shallow lakes, etc., but it is a slow process in North Sweden, and is often counteracted by erosion. A »water shore» community usually formed by *Menyanthes* and *Carex rostrata*, rooting in the »land shore» and stretching into the water, is often important in this process, which results in a slowly advancing, very irregular shoreline, leaving small almost overgrown holes with open water behind it as dangerous pitfalls.

The other communities of wet, loose peat are the carpets and the mud-bottoms, wich (together with the lawns) are parvocariceta, dominated by less tall and not very dense sedges, and the like. Floristically they are more related to the tall sedge communities than

to the lawns; most of the tall mire graminids occur in the carpets and mud-bottoms, too, but not in large quantities.

The carpets are very closely related floristically to the mud-bottoms, as almost all the species of the field layer may occur in both. A notable exception is *Carex pauciflora*, which is a lawn and hummock species sometimes occurring in carpets but almost totally absent in typical mud-bottoms. The most common dominants, all of which occur in both poor and rich fen carpets, are *Carex limosa*, *C. chordorrhiza*, *C. livida*, *Scheuchzeria palustris*, *Menyanthes trifoliata*, and in the S and SE *Rhynchospora alba*. Often dominating although not growing densely are *Carex rostrata*, *C. lasiocarpa*, *Equisetum fluviatile*, *Eriophorum angustifolium*, and *Phragmites communis*. The communities formed by them lead over to the magnocariceta. Communities with *Eriophorum vaginatum* lead over to the lawns. In margin and spring fen carpets we meet with *Carex fusca*, *C. magellanica*, *C. canescens*, *Equisetum palustre*, *Potentilla palustris*, *Calamagrostis purpurea*, *C. canescens* (mainly in the S and SE), and others. *Carex diandra* and *C. heleonastes* and a few others are sometimes found in rich fens. On the whole, the field layer species of the carpets are less numerous than those of the lawns occupying the same position in the poor fen—rich fen series.

The bottom layer is always well-developed but usually includes only few species. The difference between typical poor fen and rich fen is very pronounced, but transitions occur. The poor fen carpets are characterized by soft, low *Sphagnum* vegetation, formed by *S. Dusenii*, *S. Lindbergii*, *S. apiculatum*, *S. pulchrum*, *S. Jensenii*, *S. Aongstroemii*, etc., in wetter stages, and commonly *S. papillosum* (sometimes *S. magellanicum*, *S. parviflorum*, etc.) in drier stages; the latter bottom layer synusia resemble those of the lawns, but are here combined with a field layer more or less different from that of the lawns (although transitions occur, of course). In transitional poor fen carpets *Sphagnum subsecundum* is usually present, and in mire margins *S. riparium*, too. In intermediate fens we also find *Calliergon sarmentosum*, *Drepanocladus procerus*, *D. purpurascens*, *D. revolvens*, *Riccardia pinguis*, *Sphagnum auriculatum*, *S. platyphyllum*, and *S. inundatum*; sometimes also in somewhat drier stages *Drepanocladus badius*, *Sphagnum plumulosum*, *S. subfulvum*, *S. Warnstorffianum*, *S. centrale*, together with *S. papillosum*. These species are more typical of the lawns, however.

In the rich fens proper, *Scorpidium scorpioides* is always a prominent dominant of the bottom layer of the carpets. Other species are

*Cinclidium stygium*, *Calliergon trifarium*, *Meesia triquetra*, etc. In somewhat drier parts *Drepanocladus intermedius* and sometimes *Paludella squarrosa*, *Campylium stellatum*, etc., prevail, leading over to lawns with a similar bottom layer (cf. p. 194). In springs we partly find other bryophytes in the carpets, e.g. *Scapania uliginosa*, *Riccardia multifida*, *Chiloscyphus fragilis*, *Philonotis fontana*, *Ph. tomentella*, *Ph. seriata*, and *Anisothecium squarrosum* in non-calcareous springs; *Webera* (*Mniobryum*) *albicans* v. *glacialis*, mainly in the mountains, in probably slightly calcareous springs (together with several of the species mentioned); and *Cratoneurum decipiens*, *C. commutatum*, *C. falcatum*, *C. filicinum*, and *Philonotis calcarea* in strongly calcareous springs Cf. p. 190.

The carpets are soft, loose and often quaking. Probably they are dependent on a comparatively constant and high relative water-table, such as is most likely to occur when the mire surface follows the fluctuations of the water-table to a certain extent (where the peat is elastic, according to KULCZYŃSKI 1949). On very wet but not quaking soil, they are usually replaced by mud-bottoms, which are by far more common in N Sweden, esp. in the fen areas developed through peat formation directly on mineral soil. These are much more extensive here than are the parts of the fens formed by choking up of the bodies of water. The carpets are concentrated to the latter parts, being mainly located along the shores of small tarns and lakes or covering deep depressions in the underlying mineral ground. In addition, carpets are found in those parts of the fens which are strongly watered by springs.

The mud-bottoms are similar, with regard to the field layer, to the carpets, although the vascular plants often grow more scattered and sometimes are absent altogether. On the other hand, a few species are more or less specialized mud-bottom dwellers. Some of them occur outside the mires on wet mineral soil with sparse vegetation, esp. in the »eulitoral» belt of the oligotrophic lakes, e.g. *Lycopodium inundatum*, *Rhynchospora fusca*, *Drosera intermedia* (these mainly or only in the S and SE), and *Juncus alpinus* ssp. *nodulosus* (cf. WALDHEIM 1944 p. 38). Others occur in lakes as water plants (*Nymphaea*, mainly *N. candida*, *Utricularia intermedia*, *U. minor*, *Sparganium hyperboreum*). Almost »characteristic» species of the fen mud-bottoms are *Juncus stygius* and *Eriophorum medium*. The most common dominants in the mud-bottoms are *Carex limosa*, *C. chordorrhiza*, *C. livida*, *C. rostrata*, *C. lasiocarpa*, *Scheuchzeria palustris*, *Eriophorum angustifolium*, *E. medium* (in the NE), *Menyanthes trifoliata*, *Rhynchospora alba* (in the S and SE), and *Equisetum fluviatile*. Of other species may be mentioned

*Drosera anglica*, *Eriophorum gracile*, *Hammarbya paludosa*, *Carex panicea*, *Calamagrostis neglecta*, *Phragmites communis*, all of which with the exception of the first-mentioned are absent in the mud-bottoms of the poor fens proper. In rich fens we may sometimes also find *Triglochin palustre*, *Carex heleonastes*, *C. diandra*, *Equisetum scirpoides*; in extreme rich fens also *Salix myrsinites*, *Carex jemtlandica*. In addition there are often species more typical of lawns, for instance *Scirpus caespitosus*, *Eriophorum vaginatum* (mostly in poor fens) and *Scirpus Hudsonianus* (mostly in rich fens).

The bryophyte bottom layer of the mud-bottoms is always very scanty, being replaced by a micro layer of algae, or sometimes iron bacteria. This is the main difference from the carpets. Floristically, however, the difference is not very great, as the same species of bryophytes are present. In mud-bottoms the bryophytes are loose-lying, because of which even the orthotropic species generally grow horizontally. The most common bryophytes are probably: in extreme poor fens *Sphagnum compactum*, *S. Lindbergii*, *S. Dusenii*, *Drepanocladus fluitans*, *Gymnocolea inflata*, *Cladopodiella fluitans*; in transitional poor fens also *Sphagnum subsecundum*; in intermediate fens also *Calliergon sarmentosum*, *Drepanocladus procerus*, *Riccardia pinguis* (in transitions to lawns *Odontoschisma elongatum*); in rich fens above all *Scorpidium scorpioides*. Bryophytes may be entirely absent over large areas. Sometimes all macrophytes are lacking, and the mud lies bare.

The mud is composed by alga and detritus mud (Sw. *gyttja*) often more or less contaminated with precipitated humus (Sw. *dy*). Iron ochre occurs very frequently in N Sweden (not so frequently in calcareous districts and in the mountains) and is formed in mud-bottoms where pH is not too low (usually more than 5), and probably originally oxygen-free subsoil water, having been in contact with the mineral soil, is exposed to the air. In calcareous fens we may find deposits of calcium carbonate (Sw. *bleke*) as a thin crust on the bottom and on the bryophytes. The latter two sediments are generally not permanent, as the minerals are dissolved again.

Mud-bottoms are very extensive in the N Swedish fens. They are mostly developed as »flarks» (see below p. 210) though sometimes occupying whole mires or parts of mires. The water-table is high in wet periods, esp. in springtime, but sometimes in droughthy summers the mud-bottoms dry up almost completely. This is, however, exceptional. It seems probable that mud-bottoms are less dependent on the elasticity of the peat than carpets, but there are also mud-bottoms on very



quaking soil. The competition between bryophytes and algae may be important as a distinguishing factor between carpets and mud-bottoms, as I have suggested (1946 b p. 61). The area covered by mud-bottoms increases towards higher altitudes and towards the N. A short vegetation period may be important as a condition limiting the growth of the bryophytes. Also the very sudden and short springs with the strong accumulation of thawing-water in the fens may impede the bryophytes and promote the mud-bottoms.

**Properties of the root-systems.** It was already stated in my previous paper (1948 a pp. 62—63) that most (but not all) graminids (DU RIETZ 1921 b) of the lawns are more or less caespitose hemicryptophytes. Part of the lawn graminids and most of the lawn herbs spread their roots in the superficial layer of the peat that is not totally waterlogged. The graminids of the carpets (and also of the magnocariceta and mud-bottoms) as a rule have rather deeply located, creeping subterranean stems, sending up single aerial shoots. The subterranean stems, and most of the roots, spread within the zone of total waterlogging of the peat. It was also stated (pp. 253, 288) that species normally forming mycorrhiza are confined to those parts of the mires which have a superficial stratum containing oxygen, and that in the other parts the field layer is mainly made up by species with aerenchyme in their subterranean parts. Reference was made to METSÄVAINIO (1931).

From his investigation of the root-systems of numerous mire plants I have now compiled Table 1. The Table serves two purposes, first to give an account of the principal preferential species of the hummocks, lawns, etc. (for which purpose the most important of the species not investigated by METSÄVAINIO are added above the Table), and secondly to show the correlations between the grouping and certain properties of the root-systems.

All species that penetrate to any considerable depth are provided with aerenchyme, but a few plants with aerenchyme are shallow-rooted (*Empetrum*, *Drosera* spp., *Pinguicula vulgaris*, *Pedicularis* spp., *Carex capillaris*). Aerenchyme is found in all the plants of magnocariceta, carpets, and mud-bottoms, with the exception of the shallow-rooting *Andromeda* and *Oxycoccus quadripetalus*, and in many of the species of lawns and hummocks, too, e.g. in all *Cyperaceae*. The deepest rooting is found among the species preferring the magnocariceta and the carpets, whereas the mud-bottoms seem to be preferred by plants with less deep rooting, although most of the former species are also able to live in them. There is much more variety in the behaviour of hummock and lawn plants. Some of them root deeply or even very deeply (*Carex globularis*, *Rubus Chamaemorus*, *Cirsium palustre*, *Eriophorum latifolium*, *E. vaginatum*, *Molinia*), others are entirely confined to the superficial more or less aerated peat (*Ericaceae*, *Maianthemum*, *Orchidaceae*, *Parnassia*, *Trientalis*, *Viola palustris*, etc.). The occurrence of such species as *Geum rivale*, *Maianthemum* and *Viola palustris* in spring fen carpets is probably due to the oxygen dissolved in the water, allowing the roots to penetrate into the ground water.

**Table 1.** Some preferential species of different kinds of mire communities, and some properties of their root-systems according to METSÄVAINIO (1931). \* = a decided preferential species. Depth = penetration of roots below ordinary ground water level. Aer. = presence of aerenchyme in subterranean stems and roots. Myc. = presence of mycorrhiza.

The following species which were not included in METSÄVAINIO's investigation may be added. Lawns preferred: *\*Bartsia alpina*, *\*Juniperus communis*, *Myrica Gale*, *\*Narthecium ossifragum*, *\*Potentilla erecta*, *\*Saussurea alpina*, *\*Schoenus ferrugineus*, *\*Selaginella Selaginoides*, *\*Succisa pratensis*, *\*Thalictrum alpinum*, *\*Tofieldia pusilla*. Lawns and carpets, mostly the former: various *Salices*. Mud-bottoms preferred: *Carex livida*, *\*Eriophorum medium*, *Hammarbya paludosa*, *\*Lycopodium inundatum*, *\*Rhynchospora fusca*, *\*Utricularia intermedia*, *\*U. minor* (the latter two rootless).

	Depth	Aer.	Myc.
<b>Hummocks preferred:</b>			
<i>Betula nana</i> .....	(+)	(+)	+
<i>*Calluna vulgaris</i> .....	—	—	+
<i>*Carex globularis</i> .....	++	+	—
<i>*Drosera rotundifolia</i> .....	—	+	—
<i>*Empetrum</i> .....	—	+	+
<i>Equisetum silvaticum</i> .....	+	+	—
<i>*Ledum palustre</i> .....	—	—	+
<i>*Oxycoccus microcarpus</i> .....	—	—	+
<i>Rubus Chamaemorus</i> .....	++	+	+
<i>*Vaccinium Myrtillus</i> .....	(+)	—	+
— <i>uliginosum</i> .....	(+)	—	+
<i>*— Vitis-idaea</i> .....	—	—	+
<b>Lawns preferred:</b>			
<i>Andromeda Polifolia</i> .....	(+)	—	+
<i>*Angelica silvestris</i> .....	—	—	—
<i>*Carex capillaris</i> .....	—	+	—
<i>*— dioeca</i> .....	+	+	(+)
— <i>echinata</i> .....	+	+	—
<i>*— flava</i> .....	+	+	+
— <i>loliacea</i> .....	+	+	—
— <i>pauciflora</i> .....	+	+	—
<i>*— vaginata</i> .....	+	+	—
<i>Cirsium palustre</i> .....	++	+	—
<i>Crepis paludosa</i> .....	(+)	—	—
<i>Eriophorum latifolium</i> .....	++	+	—
— <i>vaginatum</i> .....	++	+	—
<i>Filipendula Ulmaria</i> .....	+	(+)	—
<i>Geum rivale</i> .....	—	—	—
<i>Juncus filiformis</i> .....	+	+	—
<i>*Maianthemum bifolium</i> .....	—	—	+
<i>*Molinia coerulea</i> .....	++	+	+
<i>*Nardus stricta</i> .....	+	+	+

	Depth	Aer.	Myc.
*Orchidaceae .....	—	—	+
*Parnassia palustris .....	—	—	+
*Pedicularis Sceptrum-Carolinum .....	—	+	—
Peucedanum palustre .....	(+)	+	—
*Pinguicula vulgaris .....	—	+	—
*Rubus arcticus .....	—	—	+
*Scirpus caespitosus .....	+	+	+
*— Hudsonianus .....	+	+	(+)
Solidago Virgaurea .....	—	—	—
*Trientalis europaea .....	—	—	—
Viola palustris .....	—	—	—

**Lawns and carpets equally:**

Carex canescens .....	+(+)	+	—
— fusca .....	++	+	—
— panicea .....	+	+	+
Oxycoccus quadripetalus .....	(+)	—	+

**Magnocariceta preferred:**

Calamagrostis purpurea .....	++	+	—
*Carex aquatilis .....	+	+	—
— caespitosa .....	++	+	—
— juncella .....	++	+	—
— lasiocarpa .....	++	+	—
— rostrata .....	++	+	—
Equisetum fluviatile .....	+++	+	—
Lysimachia thyrsiflora .....	+	+	—
Menyanthes trifoliata .....	++	+	—
Phragmites communis .....	+++	+	—
Potentilla palustris .....	++	+	(+)

**Carpets preferred:**

Carex magellanica .....	+(+)	+	—
Equisetum palustre .....	++	+	—
Scheuchzeria palustris .....	+(+)	+	—

**Carpets and mud-bottoms equally:**

Carex chordorrhiza .....	+	+	—
- diandra .....	+	+	—
* - limosa .....	+(+)	+	—
Eriophorum angustifolium .....	++	+	—
*Pedicularis palustris .....	(+)	+	—

**Mud-bottoms preferred:**

Carex heleonastes .....	+	+	—
Drosera anglica .....	—	+	—
Eriophorum gracile .....	+	+	—
*Juncus stygius .....	+	+	—
Rhynchospora alba .....	+	+	—

Mycorrhiza is absent in all the plants of the magnocariceta, the carpets and the mud-bottoms, with the exception of the shallow-rooting ericaceous plants *Andromeda* and *Oxycoccus*, *Carex panicea*, which seems to have most roots very near the surface, the facultatively mycorrhiza-forming *Potentilla palustris*, and the extremely shallow-rooting orchid *Hammarbya* (*Malaxis*) *paludosa*, which was not investigated by METSÄVAINIO. In the lawns, many of the investigated species have mycorrhiza, besides the *Ericaceae* and the *Orchidaceae* for instance *Carex flava*, *Maianthemum*, *Molinia*, *Nardus*, *Par-nassia*, *Scirpus caespitosus*. *Rubus Chamaemorus* and all the dwarf-shrubs of the hummocks have also mycorrhiza. — For further information and for a comprehensive bibliography, reference is made to METSÄVAINIO; the mycorrhiza of trees and tree seedlings in mires was investigated by MELIN (1917). Recent advance in the study of air in roots is due to IVERSEN (1949).

It is thus quite evident that certain properties of the root-system restrict many plants to a limited range of habitats in the mires, and that this is one of the reasons for the differentiation into the vegetational series dealt with in this section.

### Local geographical differentiation within the mires.

In my previous treatise (1948 a pp. 46—53) I gave an account of the geographical differentiation found in a mire. For the sake of brevity, the definitions of the concepts introduced cannot be repeated here; short definitions in English were given on p. 280. The most prominent mire features of N Sweden are the same as in Bergslagen (Il.cc.); the p a l s e s in the northernmost mires (see below p. 213) may be added.

The mires are composed of large or small areas of which some may have a uniform structure (being a single large feature) and others may show a pattern of more or less regularly alternating features. Whether compound or not, these larger areas, which together constitute the big mire complex, are termed mire sites (site according to BOURNE 1931, who used this term in about the same meaning as TROLL's *Landschaftselement*, e.g. 1942). A mire site should not be too different in its different parts; if it is compound, the components should be the same all over the site. A mire feature may be regarded as a simple holocoen in the sense used by FRIEDERICHs (1937 pp. 17 ff.), THIENEMANN (1941 p. 111) and JULIN (1949 pp. 136 138, 182 183); a site is a larger holocoen or mostly a holocoen complex. Because the substrate is included, a feature or site is not a plant community, nor a vegetation complex; the concepts are geographical, not purely biocoenological.



Du RIETZ has recently (1949) advocated the opinion (different from that maintained in his earlier works) that the vegetation of the compound mire sites should be regarded as plant communities of a superior rank to their components. It seems, however, more natural to unite the vegetation of each component with similar vegetation elsewhere as a plant community, thus using similarity in composition as the leading principle in phytosociology. The units kept together mainly through characters of location and arrangement are better regarded as geographical objects than as plant communities.

The most characteristic property of a mire site is its hydrotopography, and the origin of the water feeding it. According to v. POST & GRANLUND (1926 pp. 63—64) the mires may be classified as ombrogenous, topogenous, or soligenous. It was stated (l.c.) that in many cases the mires are compound with regard to these categories (cf. also HALDEN 1934 p. 48). The concepts were re-defined by me (1948 a pp. 42—46, 279) on the basis of hydrotopography only. The »wet of soil» (l.c.) and the corresponding mire sites may be »regarded as topogenous, if the mineral soil water surface causing wet of soil is approximately horizontal; as soligenous, if the mineral soil water causes wet of soil while still in motion, i.e. while the subsoil water surface is distinctly sloping. This classification applies to springs as well as diffuse outlets of subsoil water». The ombrogenous wet of soil is »caused by subsoil water derived from precipitation only» (p. 279). In addition, the »wet of soil caused by inundation or permanent influence of water from rivers and lakes» was termed limnogenous (l.c.); its properties are closely related to those of the topogenous »wet of soil».

The North Swedish mire sites may be grouped according to these concepts. In addition to the pure groups, we have in North Sweden also mire sites that are compound with respect to »wet of soil», viz. those with ombrogenous moss hummocks and soligenous (sometimes almost topogenous) wet fen between them, the so-called »mixed mires» (or better: mixed mire sites, because they as a rule do not occupy the whole mires).

### Ombrogenous mire sites.

Ombrogenous parts of mires are in practice identical with mosses (bogs), although the definition of the former is hydrotopographical, of the latter phytosociological. We have already spoken of wooded and open moss sites and their regional distribution. In the mire complexes, the wooded moss sites occupy various positions. We find them as mar-

ginal forest around the mosses built up concentrically (in the SE; pp. 214–215) but also along the edges of the unilaterally sloping or otherwise eccentrically developed mosses that prevail in Bergslagen and some other districts. In the latter they are found both in the proximal (upper) and the distal (lower) position. If there are »soaks» (narrow soligenous mire sites) running downward these slopes, wooded moss is usually found between the upper parts of the soaks. If the soaks widen to form broad soligenous fens we often find marginal islands of wooded moss between the proximal water tracks or sheltered by ridges of mineral soil. In regularly cup-shaped mire basins in not too humid districts, the wooded moss islands may form a marginal ring broken at intervals around a central pure fen site (the *Ringhochmoore* or marginal mosses of OSVALD 1925 p. 719, 1949 p. 14).

Open moss sites composed only by hummocks are found on shallow peat and are often strongly sloping. Transitions to damp heath are found in the mountains and also in the upper coniferous forest sub-region of some high hills outside the Scandes proper (e.g. in Lima parish, Dalarna). A narrow belt of treeless open hummocks is often found adjacent to the proximal (upper) marginal forest in unilaterally sloping mosses.

Most large open moss sites are provided with hollows. The hummocks form a network with the hollows in the meshes. If the surface is sloping, both hummocks and hollows are extended at right angles to the slope. The hummocks form longish banks. The hummock-and-hollow sites are of different kinds according to the development of the hollows — as lawns, carpets, or mud-bottoms. The sites with lawn hollows have as a rule a more marginal location, and such a site may occupy the whole open area of certain small mosses. In the highly humid districts these sites are replaced by sites with both lawns and mud-bottoms in the hollows, probably on less elastic peat than the sites with carpet hollows. In the large mosses, mud-bottoms usually prevail over large areas in the hollows. Cf. p. 184.

It seems possible that lawn hollows are dependent on a moderate water content of the moss site, whereas both mud-bottom and carpet hollows depend on a very high water content, in the carpet hollows with a surface that is able to follow the fluctuations of the ground water level to a greater extent through rising and sinking (Sjörs 1948 a p. 92). This is an application of KULCZYŃSKI's theories (1949) on our N Swedish mosses, but needs more observational confirmation.

### Topogenous and limnogenous mire sites.

Topogenous and limnogenous sites are occupied by fen vegetation, because their water has in part come from the surrounding mineral soil or from watercourses chiefly fed by water from mineral soils. The sites that are regularly submerged at high water are as a rule occupied by magnocaricetum or sometimes mud-bottom vegetation, those that are submerged less frequently have carpet vegetation, or, on thin or firm peat and along the margins, sometimes lawn vegetation. The rule seems to hold good also in this case that true carpets are dependent on the elastic conditions of the peat. The most typical and extensive of the North Swedish fen carpets are probably developed over deep depressions in the underlying mineral soil, covered by loose, quaking or even floating peat, or on similar peat along the shores of tarns and lakes.

Topogenous fen sites are extensive only in the less humid SE parts, including the lower parts of the river valleys. In the other, more humid districts, soligenous fens prevail, and topogenous fens only occur locally. However, in flat country in Central and North-Eastern Norrland, for instance in some parts of the Cambro-Silurian of Jämtland and in the Central Muddus plain, we find large soligenous fen sites so slightly sloping that they may almost be regarded as topogenous. They occupy a central position in the large »aapa» mire complexes (see p. 216). As brooks, tarns and small lakes often occur, they may in many cases be regarded as limnogenous as well. The limnogenous fens proper may in some cases occupy large areas, as in flat sedimentary basins, for instance in the valley and delta of the river Enan in W Jämtland and at the mouths of certain other streams also falling into Lake Änn.

### Soligenous mire sites.

The soligenous sites are also occupied by fen vegetation. In some cases, transitional between ombrogenous and soligenous sites, the influence of mineral soil water is very slight and the vegetation is similar to that of moss hollows (usually lawns), but contains some species or other indicative of the fens (e.g. *Carex pauciflora*).

The soligenous fen sites are very extensive in the N Swedish mires. The differentiation of the soligenous sites and the positions taken up by them in the mire complexes are very variable. It is difficult to give an account of these imperfectly known conditions.

Whereas soligenous magnocariceta and carpets are of little importance quantitatively (in springs, on strongly irrigated slopes below springs and in other strong water tracks, in wet basins where the surface is only slightly sloping, and sometimes as transitions between magnocariceta and lawns replacing the latter), we find, as normal soligenous sites, fen hummock land, lawns, and the combination of lawns and mud-bottoms. The order is that of increasing water content, i.e. of the water-flow in relation to its velocity. Thus, in fen hummock sites, the flow of water is extremely small, in lawns either small and slow or rather large and rapid, and in the combination of lawns and mud-bottoms large and slow, or sometimes very large and rather rapid. The velocity of the soligenous water-flow is dependent on the slope and the resistance, the latter of which is enormously great in hummocks with highly humified peat, moderate in lawns and practically none in mud-bottoms (cf. MALMSTRÖM 1923 pp. 109—115), and always decreasing with increasing water-flow. In the formation of the types of sites mentioned, the soligenous fens (the sloping mosses are analogous) possess a self-regulating mechanism, by means of which the mire adopts itself to the amount of water that has to pass its various parts. I have dealt more in detail with these phenomena before (1946 b pp. 62—63, 91, 1948 a p. 263) so that a closer discussion is superfluous here.

The fen hummock sites have been dealt with above (p. 195). Common types of sites are also fen hummocks with small patches or »windows» of wetter fen (lawns, carpets or mud-bottoms) or with »boulder-pits» (see above pp. 180, 196). These sites are impossible to separate sharply from the corresponding types of »mixed mire» (p. 211) in which the hummock component is true moss.

The pure lawn sites are chiefly found in sloping hillside fens. In moderately humid districts, for example in Central Jämtland, Västerbotten (MALMSTRÖM 1923), and Muddus, they are of local importance. In the humid parts of Bergslagen and NW Dalarna, and still more in W Jämtland and W Lappland, these sloping lawns are extensive. The »smooth sloping fens» (SJÖRS 1946 b) are found in all parts of the hill-sides where the flow of soligenous water reaches the surface. In the most humid district, the slope may be 1 : 5 and sometimes even more (1 : 2.5 locally).

These sites are dependent on a moderate flow or a quick run-off of the water. In the former case the soligenous influence is small, for instance in some marginal parts of the sloping fens, or where most of the water has gathered through brooks or other water tracks, or in



the shelter of mineral soil islands. In such places the vegetation is usually poor fen lawns. In the strongly sloping lawns with a large water-flow the vegetation is chiefly intermediate fen (on poor mineral soils), or rich fen (extreme rich fen on strongly calcareous soil). These conditions are, however, very complicated, because of the different proportions between ombrogenous and soligenous water and the different properties of the latter, which vary according to the primary composition and the podsolization and leaching of the soil strata from which it is derived.

Thus a map of the distribution of different grades of richness in species will not always give a clear picture or one that is easy to interpret (moreover, it needs a very large scale and is very difficult to construct), in contrast to a map of the lawns, mud-bottoms, etc., which even in such a small scale as about 1 : 10000 or even 1 : 20000 gives very good information on the hydro-topography of the mire and its nearest surroundings. Such a map can easily be constructed with aid of air pictures, on which the lawns, mud-bottoms, and other features are visible, and the mire sites formed by them may be made out after simple field reconnoitring, or, with some experience, even without field work. Cf. SJÖRS 1948 a, esp. the Maps and Plates.

The sites with lawns and mud-bottoms in combination are very extensive in wet soligenous fens. The lawns form long, low banks damming the mud-bottoms or »flarks» which form horizontal platforms or stairs in the fen staircase. Sites with flarks are widespread in North Sweden with the exception of the non-humid SE valleys and coastal belt. They have not been found in South Sweden, but other sites with mud-bottoms occur, for instance a type with a network of mud-bottoms, also found sometimes in North Sweden. The slighter the slope or the larger the water-flow, the greater is the percentage of the area taken up by the mud-bottoms. These sites occupy the strong water tracks and usually widen to form large »flark» complexes in the central parts of the soligenous fens. Carpets may sometimes be present, in part as transitions between the mud-bottoms and the lawns (not important), in part covering certain parts with loose, quaking peat. It seems probable that these »flark» sites are mainly formed on rather thin peat, where the fluctuations in water level cannot be compensated by the rising and falling of the surface to any considerable extent. Erosion of the peat, probably also superficial oxidation, takes place in some mud-bottom sites. Not unfrequently the mineral soil lies bare in certain flarks. — There is an extensive literature on the flarks which has been quoted in my earlier works (1946 b pp. 56—65, 1948 a p. 139).

### Mixed mire sites.

»Mixed mire» (Sw. *blandmyr*) refers to mire sites with a mixture of moss (bog) features — always hummocks — and fen features of different kinds. There are five main types of such sites, viz. the soak network type, the fen »window» type, the moss island type, the moss bank or »ribbed» type, and the »pals» type.

The soak network is a rare but interesting kind of mixed mire site, which differs from all the other kinds in the direction of extension of the components, these latter being extended in the direction of the slope. The moss hummocks, sometimes with pine forest, form low ridges between narrow tracks of soligenous fen (»soaks») which are frequently united by way of anastomosis, forming a network with elongate meshes. Further notes in SJÖRS 1948 a (pp. 70, 109, 265, Pl. 23). This type of site is found where a strong soligenous water-flow is split up into numerous water tracks; it may be regarded as a concentration in a small area of the type of mire complex consisting of sloping mosses separated by soligenous fen »soaks» and spoken of below (p. 215). It is not at all related to the other kinds of mixed mire sites.

The fen »window» type of mire site (DU RIETZ 1945 p. 22) differs from the other types in that the moss hummock component is continuous, and that the fen component occurs as isolated shallow pits or windows. In these mire sites there is no or only a very thin stratum of ombrogenous water above the bottom stratum of fen water, because of which the latter is exposed in the depressions. The peat is very shallow, and the fen windows may be replaced by »boulder-pits». As stated above (p. 180), the moss component is seldom pure and there are transitions to the more common type of site with fen hummock instead of moss. The fen window type of site occurs chiefly in the marginal parts of the mire complexes. It is probably chiefly north-eastern in distribution, being disfavoured by a too strong soligenous flow of water in the margin of the mire. For instance, such sites are widespread in Muddus, esp. in the flat central parts.

The moss island type is a common and widespread type of mixed mire site. The moss hummocks form islets which are separated by wet fen of various kinds: lawn, magnocaricetum, carpet, mud-bottom and various transitional or compound kinds of fen. Often the hummocks, or at least the small and low ones, contain fen species rooting in non-ombrogenous deeper strata. However, some of them are

as a rule covered with true moss vegetation. This is a continental type of site, although examples may be found in most parts of North Sweden (also in parts of South Sweden). In Bergslagen (SJÖRS 1948 a) this site is rarely observed (more frequent in the north-eastern parts); the same is the case in W Jämtland (SJÖRS 1946 b). In Central Jämtland we find many good examples, even on strongly calcareous soil. BOOBERG's Gisselåsmýren (1930) was for the greatest part a site of this kind, of complicated structure, including lawns with a thick »turgescens» bottom layer as well as wet, low lawns, carpets, and mud-bottoms, all calcareous, besides the hummocks which took up about 15 % of the whole analysed area. Most of these hummocks were fen, or at least contained scattered shoots of fen species (most common *Carex chordorrhiza*; see BOOBERG's Tables pp. 31—53). They were mostly longish in shape, constituting transitions to the type of hummock found in the sites spoken of in next section. — In Ångermanland (MELIN 1917), Västerbotten (MALMSTRÖM 1923), and Muddus, this kind of site is not rare. It seems to be very widespread in the mires of large parts of Finland.

Through transitions like that on the Gisselåsmýren (and also found in many other mires) the island mire sites are connected with the hummock bank or »ribbed» type of mixed mire, where the moss hummocks form very long and rather narrow banks or »ribs», separating wet fen areas in about the same way as the low lawn banks separate the flarks in the pure fen sites just spoken of above (p. 210). The banks are thus at right angles to the slope, and the wet areas between them are practically horizontal, mostly appearing as mud-bottoms (flarks) but sometimes also as lawns, magnocariceta, or carpets, as a rule only in a restricted area close to the banks. The hummock banks are about two or sometimes three feet high, and when well-developed they carry an almost pure moss (bog) vegetation. (See above, p. 181). These sites are found in slightly sloping or sometimes almost horizontal parts of the mires, and contain much water, which is in very slow motion (if the water supply is great, they are replaced by pure fen sites in which the water can move more rapidly). The slighter the slope, the more apart from each other are the banks or »ribs»; in almost horizontal sites, they are irregular and often broken. The water fluctuations are very great, with a complete inundation of the fen areas in springtime.

Regarding the development of the banks, in which raising through frost action takes an important part, see e.g. RANCKEN 1912, AUER

1920; regarding the position of these sites in the mire complexes, see SJÖRS 1946 b and 1950 a (p. 37); regarding the distribution, see LUNDQVIST 1943 (pp. 144—147). According to him, this kind of site is typically developed and very extensive chiefly in Central N Lappland and N Norrbotten. Many, as a rule less typical, examples are found elsewhere in N Sweden, chiefly, but not exclusively, in the more continental parts. In Bergslagen they are very rare and hardly typical. Better examples are known e.g. from NW Hälsingland (ROCÉN 1921 esp. p. 313) and from Västerbotten (MALMSTRÖM 1923; a good picture in MALMSTRÖM 1928 p. 303).

We need much more information about the distribution of this type of site; in the literature, it has often been overrated as a component of the N Swedish mires (e.g. DU RIETZ 1925 p. 16). Another frequently made exaggeration (DU RIETZ l.c., OSVALD 1949 p. 14) is the statement that the rib-like shape of the hummock banks should be due to a strong slope, not found in the island type; on the contrary, most typical »ribbed mires» (OSVALD l.c.) are less sloping than most of the »island mires», but it is true that in the sloping examples of the latter the islands are more or less longish. The difference is due to the fact that the »ribbed» type, occupying a lower position in the mire complex, keeps much water stagnant between the banks or ribs, whereas the »island» type is not able to store its water. The »ribbed» type becomes prominent only in regions with low temperatures and not too much snow in early winter, when strong frost action occurs in the peat, by means of which the long hummock banks are forced to rise, in a manner investigated by AUER (op. c.). In this way hummock vegetation can exist in areas that are flooded, which would otherwise not be possible.

OSVALD (1937 p. 154, 1949 p. 14) holds the view that »in calcareous districts, the moss area may be strongly reduced or totally absent. The whole mire is then a fen. On the other hand in districts with very poor mineral soils the moss areas may cover most of the peat land . . .» This has in reality little to do with lime, as we find extensive fens without a single hummock on the extremely poor soils of the Upper Långan district in Jämtland (SJÖRS 1946 b) and in many mires in non-calcareous districts elsewhere, e.g. in Bergslagen, NW Dalarna, Muddus etc., but many mixed mires in calcareous districts (e.g. the Gisselåsmýren). The important differentiating condition is the flow of mineral soil water. A high water-table, esp. of moving soligenous water, even if very dilute, much more effectively hampers the formation of moss hummocks than does a low water-table of even very strongly calcareous water.

The last type of mixed mire site is that provided with »palses». A pals is a huge hillock, frozen in the interior, which is made up by peat pressed into it from the surrounding fen through frost action. The surface is covered by moss (bog) peat, which is extremely dry in dry weather and carries a vegetation rich in lichens. I have nothing to



add to the literature on palses. The chief works on palses in Sweden are TH. C. E. FRIES & BERGSTRÖM 1910, TH. C. E. FRIES 1913 (with a theory of their development, pp. 189—201), DU RIETZ 1921 a pp. 11—13 and 1921 b pp. 160—162 (notes on vegetation), LUNDQVIST 1943 pp. 147—150 and 1948 pp. 406—413 (distribution). They are practically confined to northernmost Sweden (chiefly in the subalpine region but also in the low alpine region and the upper coniferous forest sub-region) where the pals sites to a certain extent replace the other mixed mire sites. According to LUNDQVIST, the palses need a hard winter climate with little snow, strong winds, and very low temperatures for their formation.

### Regional geographical differentiation of the North Swedish mires.

The mire sites dealt with in the preceding section unite to form large mire complexes, a term that is used here (as in SJÖRS 1948 a) in the meaning given by CAJANDER (1913 p. 50). The mire complexes are the largest and most complicated among the units of the mires, being as a rule composed by several mire sites in a more or less characteristic arrangement, and often covering very extensive tracts of land. The largest mire complexes are situated in northern Lappland, viz. the Pirttimusvuoma-Rienakvuoma complex (c. 170 sq. km) and the Ripa-kaisenvuoma complex (c. 120 sq. km) in Torne Lappmark and the Sjaunja-Jaltonape complex (c. 350 sq. km) in Lule Lappmark. Very large complexes occur also in other provinces. The large mire complexes are the most significant ones regionally but small ones are also sometimes of a certain importance.

The chief types of mire complexes are the following (cf. SJÖRS 1948 a, Chapter 6, where examples of types 1—4 are given, and Chapter 7 pp. 266—276, 289—290, with maps pp. 268—269).

1) Mire complexes mainly composed of topogenous (horizontal) fen sites. Ombrogenous or mixed sites may be present esp. along the margins. Some of these complexes are taken up by limnogenous sites to a varying extent. This type of mire complex occurs all over North Sweden.

2) Mire complexes including concentrically domed mosses with open areas in the centre, where the top of the dome is located. The lower parts of the slopes of the dome are covered with wooded moss vegetation. Slightly domed mosses entirely covered by pine wood are more common but seldom of considerable extension. The edge of the

mire usually consists of the bank of a stream or lake or of a narrow or sometimes broad fringe of topogenous fen, which is termed »lagg». These mire complexes are south-eastern in North Sweden, occurring NW of the *limes norrlandicus* only in the lower parts of SE Dalarna, Gästrikland, and SE Hälsingland. A few examples occur NW and N of this limit under special hydrotopographical conditions. They are situated on extremely flat sandy plains or surrounded on several sides by open water or resting on mineral soil that is slightly domed in itself. The first case is exemplified by the Hammarmossen (Västmanland, GRANLUND 1932 pp. 106—115, SJÖRS 1948 a pp. 189—190 and Pl. 5), the second case by the Nittenmossen (SW Dalarna, LUNDQVIST 1933 pp. 115, 120, SJÖRS 1948 a pp. 192—193 and Pl. 3), the third case by a small moss in Muddus S of Vuosmavare (SJÖRS 1946 a Pl. 2). The moss on the peninsula of Halsen at Lake Änn, W Jämtland, which was regarded as domed in SJÖRS 1948 b (p. 70), is ridge-shaped, and so is the underlying mineral soil, although irregularly.

3) Mire complexes largely consisting of mosses built up eccentrically. The mosses are usually sloping unilaterally, with the top near the margin of the mire, and with a true lagg only in places. Sometimes they are saddle-shaped, with two tops, or almost horizontal. Between the mosses there are tracks of soligenous fen called »soaks» (Sw. *dråg*), starting at the mineral soil edge and often merging into a large central soak. A large and very typical example is the Skattlösbergs Stormosse, described in detail in SJÖRS 1948 a; numerous additional examples from Bergslagen are given in the same work (cf. also SJÖRS 1949 c and d, 1950 a pp. 13—23, 1950 b). Similar mire complexes are found in Värmland and in SW Sweden, with exception of the coast and the lowland around Lake Vänern. Examples in v. POST & GRANLUND 1926, v. POST 1927 (pp. 35, 38), GRANLUND 1932, OSVALD 1925 p. 714 (»*Flach-Hochmoore*»), 1930 pp. 130—134 (»*planmossar*» and »*skålmossar*», i.e. flat mosses and concave mosses), 1937 (pp. 98—100, 103, 187), 1949 (p. 13), SJÖRS 1950 b, etc. Some of the mires visited by SMITH (1918, 1919) and RCCÉN (1920) in Gästrikland and E Hälsingland belong here. The same kind of moss is found within many W Jämtland mire complexes (SJÖRS 1946 b pp. 22—24; 1948 b pp. 69—70). A few scattered examples from other parts of Norrland have already been mentioned (p. 183). These mires are favoured by the gravelly or sandy soils (cf. below) of glaci-fluvial and glaci-lacustrine deposits and ablation moraine, maps of which are given by GRANLUND & LUND-

QVIST (1942, also appearing in LUNDQVIST 1943) and LUNDQVIST (1942 p. 124, 1943 p. 25).

4) Mire complexes mainly composed of soligenous (sloping) fen sites. In many of these mire complexes we find ombrogenous sites between the proximal parts of the water tracks and in other sheltered positions. If these sites are well-developed, we have an example of OSVALD's »marginal moss». Mixed mire sites may also be present. Examples of this type of mire complex are given in most works dealing with N Swedish mires. They are favoured by long and even slopes, by mineral soils slightly permeable to water, and by a very humid climate, which conditions all disfavour the mosses, as they tend to enlarge the water tracks (SJÖRS 1948 a pp. 271, 290). — These complexes are common all over N Sweden with exception of the lower SE parts, including the lower river valleys. They are also found in SW Sweden, where they are of importance locally, e.g. at Tönnersjö, Halland (v. POST & GRANLUND 1926, v. POST 1927, GRANLUND 1932, MALMSTRÖM 1937).

An extreme type is characterized by the very strong slopes that occur in the fens. Whole complexes of this kind are mainly restricted to the upper coniferous forest sub-region and the lower part of the subalpine region, and are very common in those parts of the Scandes that are exposed to the Atlantic west winds and have a very high precipitation. Cf. p. 209; also SELANDER 1950 (Pl. 7 and p. 154).

It is at present impossible to give a sharp general distinction between the typical mire complexes of class (4) and those in which the mixed sites play a great part. Probably a type with large areas of »island» mire sites or sites with short hummock banks may be distinguished. A more striking type is that provided with large sites of »ribbed» mixed mire (see above pp. 212—213, also regarding distribution). It is very important that we do not confuse with each other the very different kinds of »ribbed» sites (Sw. »*strängmyrar*»), viz. the pure fen sites composed of flarks and low grass-grown banks, the sloping pure moss sites composed of true moss hollows and long hummock banks, and the mixed »ribbed» mire sites composed of fen flarks and very long moss hummock banks. Very large mire complexes consisting of the latter sites and also of several other kinds of sites, esp. large wet pure fens in a central position, are the typical *aapas* of CAJANDER (1913) and his followers (cf. also SJÖRS 1950 a p. 37). They are characteristic of very flat country. In Muddus, they are found on the central moraine plain, but missing in the hilly parts and also on the Urtemjaure ablation moraine in the SE. It is against CAJANDER's intentions to

use this term for all the »Norrland mires» (V. POST 1933), or for »mixed» mire sites only. As the dominant type of mire complex, the true *aapas* are north-eastern. Still more to the north, we find mire complexes with »pals» sites, too (cf. above, pp. 213—214).

It is at present impossible to map the distribution of the different kinds of mire complexes, or the regions in which some of them are of importance or dominating, except in a very preliminary and schematic way, as was pointed out in a letter to me by Dr. GÖSTA LUNDQVIST. But such a schematic map would give the wrong idea of a regular zonation, not found in nature. In a limited area, as in Skog parish, SE Hälsingland (HALDEN 1944), or around Enafors and Lake Ånn in W Jämtland, or in Muddus, we often have several kinds of mire complexes with a sharply marked local distribution. In a similar way, local topography, local distribution of different kinds of mineral soil, and local climate, esp. precipitation and humidity, affect the mire complexes to such a degree that broad regional traits are often difficult to distinguish. If introduced on a schematic map, they would, through the very great abstraction involved, even give a misleading picture, in which, for instance, the great difference between the valleys and the adjacent uplands would be lost. The danger of being too schematic lurks in most geographical work, and especially in the work concerning a country with a broken topography, as North Sweden.

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## Some interesting vegetation types on the northern side of Torneträsk.

(Preliminary report.)

By ÅKE PERSSON and HANS RUNEMARK.

Lake Torneträsk is situated in the north of Lapland at about 67° northern latitude. The lake is situated 342 m s.m. and is about 80 kilometres long. It has its outlet through Torne älv in the east. The valley has communication with the Norwegian coastal district through a narrow pass (412 m s.m.) at Pålnoviken (an old outlet when Torneträsk was dammed by ice from the east during the latest part of the glacial period) and a broader pass at Riksgränsen (circa 500 m s.m.).

The northern side of the Torneträsk district consists of a rather steep declivity down towards the lake from a mountain district with peaks between 1000 and 1600 metres high. The forest limit is here situated at a height of about 600 metres (FRIES, 1913). The whole wooded area is situated within the regio subalpina and forms a border along the shore having a width of 1—5 kilometres, only furthest to the east is it somewhat broader. With regard to the distribution of meadow-forests and heath-forests, see Fig. 2. The distribution of the meadow-forests coincides at some extent with the appearance of calciferous bedrock (dolomites and calcareous schists), whereas the heath-forests are chiefly limited to the Archaean rock and hard schist areas.

The precipitation conditions of the district are very little known. The western part of lake Torneträsk has a rather oceanic climate, while the eastern part forms an outpost of the continental Karesuando district. By way of conjecture the precipitation at Pålnoviken may be estimated at 800 mm a year and at Laimoviken at 400 mm.

In 1948 and 1949 we undertook an investigation into the flora of an area from Pålnoviken to Tuoptijokk, on the northern side of Torneträsk, in 1948 together with ULLA CLAEISSON, SVEN ELLERSTRÖM, MARGA-

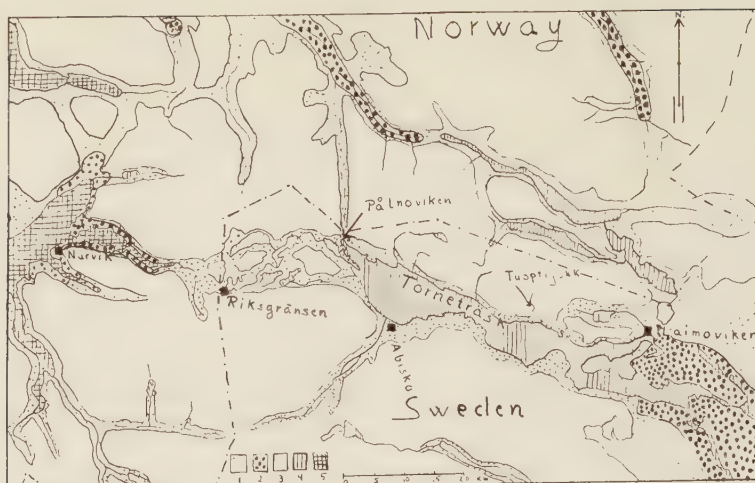


Fig. 1. Schematic map showing the Torneträsk and the Narvik districts with the valleys which join them (the distribution of *Pinus* forests around Narvik is somewhat uncertain). — 1. Subalpine *Betula* forests. 2. *Pinus* forests (regio silvatica). 3. Regio alpina. 4. Lakes. 5. The Atlantic Ocean.

RETA NORLIN and VOLKMAR STÖY and in 1949 together with ARNE GUSTAVSSON, ELSA HALLESJÖ, KERSTIN SVALANDER and BENGT ULF. The result of this investigation is collected in an extensive card-catalogue and will be wholly published later on. Only a few characteristic and interesting types of vegetation which we have been specially interested in will be treated below.

The nomenclature agrees mainly with HYLANDER, *Förteckning över Skandinaviens växter* (1941) and, for the mosses, with JENSEN, *Skandinaviens bladmosslora* (1939).

## Mires.

(By ÅKE PERSSON.)

Among the mires on the northern side of Torneträsk bogs as well as fens are represented. The bogs do not play such an important part in this area. They belong mainly to the types of mires called mixed mires (cf. DU RIETZ 1949), which cover the greater part of the area occupied by mires in Norrland. These mixed mires form a mosaic of bogs and fens. The bog growth is spread all over the wet surface of the fen as higher and

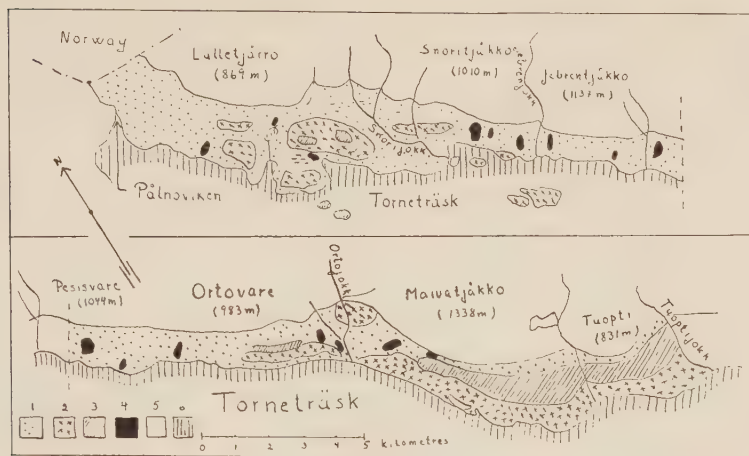


Fig. 2. Schematic map showing the investigated area in regio subalpina on the northern side of Torneträsk. — 1. Meadow forests (perhaps somewhat overrepresented on the map). 2. Heath forests. 3. Subalpine heaths. 4. »Fern forests». 5. Regio alpina. 6. Lakes.

(För publicering godkänd i rikets allmänna kartverk den 20 maj 1950.)

dryer patches. They can be formed as hummocks and as longish hummock banks. The latter are developed when the mires are strongly sloping and the hummock banks are then directed at right angles to the slope. On the northern side of Torneträsk the mixed mires are mainly to be seen in the flat area to the east of Djupviken. Here the miniature bogs can be found as small islands in the fen sections or also in connection with the surrounding mineral soil. The fens are what DU RIETZ has named »poor fens» (DU RIETZ, 1942 a, 1949). The last stage of the development of the »rich fens», to which reference will be made later on, consists of bog growth too. The bogs and the poor fens in this area have mainly the same floristical composition as other corresponding mire-types in Norrland.

From Pålnoviken in the west to Ortojokk in the east there are on the southern slopes of the mountains down to Torneträsk well developed mires with a great richness of species and a combination of species which strongly differs from the above-mentioned bogs and poor fens. These mires are situated on often very strongly sloping ground which as a consequence has a subsoil water with a great mobility. This water causes wetness of soil while still in motion (soligenous wetness of the soil).



Through weathering products from the above-lying calcareous kinds of rocks the subsoil water gets a high concentration of electrolytes and a high pH-value. In a fen at Jebrenjokk WITTING measured in the summer of 1948 in a *Scirpus pauciflorus* - *Scorpidium scorpioides* - sociation and in a *Cratoneurum falcatum* - mat the following values: Electrical conductance,  $[\chi_{20} - (\chi_H)_{20}] \cdot 10^6$ , 230 and 291, Ca-concentration, 49.6 and 58.0 mg/l, and pH 7.3 and 8.0 respectively. (WITTING, 1949 p. 734 and 729).

According to the system of DU RIETZ these mires rich in species are counted among the »extreme rich fens» in the fen subformation of the Scandes (=the Scandinavian mountain range, cf. DU RIETZ, 1949). They correspond to the eutrophic grass mires of NORDHAGEN, *Caricion atrofuscae saxatilis* (NORDHAGEN, 1943).

Among the demanding pure mountain species which are components of extreme rich fens of the area the following are worth mentioning: *Carex atrofusca*, *C. capitata*, *C. parallela*, *C. saxatilis*, *Juncus triglumis*, *Saxifraga aizoides*, *Salix myrsinites*, *Pinguicula alpina*, *Thalictrum alpinum*, *Viola biflora* and *Salix reticulata*. (See NORDHAGEN, p. 448).

There are a great many species which have not so great claims in a lower region, but which in the mountains are good indicators of a strongly nutritive substrate. Among these the following can be mentioned from this area, *Carex vaginata*, *C. flava*, *C. panicea*, *Eriophorum latifolium*, *Equisetum variegatum*, *Gymnadenia conopsea*, *Crepis paludosa*, *Festuca rubra*, *Carex dioeca*, *Scirpus Hudsonianus*, *Parnassia palustris*, *Selaginella Selaginoides* and *Angelica silvestris*. These species are characterised by a wide amplitude of pH as well as concentration of electrolytes, when their distribution in the whole of Scandinavia is taken into account. Among other species with a very wide amplitude, which in this area are important components in extreme rich fens, the following may be mentioned: *Scirpus caespitosus* ssp. *austriacus*, *Nardus stricta*, *Eriophorum vaginatum* and *Andromeda Polifolia*.

In southern Sweden *Scirpus caespitosus* is limited to bogs and poor fens. In the calcareous mires of Jämtland it is dominant together with *Schoenus ferrugineus* which has there one of its northernmost outposts. On the northern side of Torneträsk *Scirpus caespitosus* is absolutely dominant in certain types of the fens rich in species. In middle and northern Sweden *Scirpus caespitosus* is accompanied by the above mentioned *Scirpus Hudsonianus*, which may sometimes reach co-dominance.

*Nardus stricta* has a wide amplitude of pH and of concentration of electrolytes as well as of the demand of wetness. In the lower regions it is found partly in culture-influenced ground as wet and strongly cropped shore meadows, and wet as well as dry grassland poor in nutritition, partly as component in natural vegetation and then in mires of the type DU RIETZ calls »transitional poor fens» and »transitional rich fens» (WALDHEIM and WEIMARCK, 1943 and WALDHEIM, 1944). In mountain districts *Nardus stricta* can be found in strongly cropped *Agrostis*-meadows described by NORDHAGEN. As a component in natural vegetation one may find it in strongly acid *Nardus*-moors, flooded in the spring (*Nardeto-Caricion rigidae*, NORDHAGEN, 1943). It can also be found in eutrophic fens. NORDHAGEN mentions it in *Carex flava* - and *Scirpus caespitosus* - communities, which are a part of his above mentioned alliance *Caricion atrofuscae - saxatilis*. On the northern side of Torneträsk it is a component in *Scirpus caespitosus* - communities, where it can dominate on small spots. It exists only in the western parts of the area, which may depend on its oceanic tendency. The same seems to be valid for *Scirpus Hudsonianus*.

In the south of Sweden *Eriophorum vaginatum* and *Andromeda Polifolia* are typical oligotrophs. On the northern side of Torneträsk they are components of the communities most rich in species, but their frequency and vitality is small.

Among other important species being components of fens rich in species of the area might be mentioned: *Scirpus pauciflorus*, *Calamagrostis neglecta*, *Triglochin palustre*, *Pinguicula vulgaris* and *Eriophorum angustifolium*.

Among bottom-layer species may be mentioned: *Scorpidium scorpioides*, *Drepanocladus revolvens*, *Campylium stellatum*, *Tomenthypnum nitens*, *Catoscopium nigrum*, *Sphagnum Warnstorffianum*.

NORDHAGEN has pointed out a number of index species for the alliance *Caricion atrofuscae - saxatilis*. Among these species those occurring in the Torneträsk district should then be index species (and preference species) of its extreme rich fens. That is the case of e.g. *Carex atrofusca*, *Carex parallela*, *Carex capitata* and *Carex saxatilis*. On the other hand *Minuartia stricta* can not be regarded as a preference species. It has been found in fens only once. Otherwise it occurs here and there in the alpine region in schist precipices, which are dry at least in summer.

Besides there are several species, which in this area are wholly

limited to fens rich in species. Here we might mention: *Carex flava*, *C. panicea*, *Eriophorum latifolium* and *Scirpus Hudsonianus*.

In the Swedish rich fens BOOBERG, DU RIETZ and KRUSENSTJERNA have distinguished a series of unions (associations in DU RIETZ, 1949 p. 297) according to the composition of the bottom layer parallel to the changes of wetness. Such a series can also be distinguished in the fens rich in species to the north of Torneträsk.

The wettest stage has been called *Scorpidietum* after the moss *Scorpidium scorpioides*. Besides *Scorpidium* there occur within the area in the bottom layer *Drepanocladus revolvens*, *Calliergon trifarium* and *Riccardia pinguis*. The most important species in the field layer are *Scirpus pauciflorus*, *Eriophorum angustifolium* and *Triglochin palustre*. This vegetation is characteristic of »flarks». The latter consist of limited wet parts, which have been dammed up by dryer parts (peat-walls). In contrast to surrounding fen elements the flarks have a practically horizontal surface and there is often an open sheet of water. The bottom layer may sometimes be lacking.

In the series mentioned above the wettest stage is followed by less wet stages, *Drepanocladetum* and *Campylietum*. The former is characterized by *Drepanocladus intermedius*, *revolvens* or *vernicosus* as the most important bottom layer species, and the latter is dominated by *Campylium stellatum*. »These two associations run into each other, yet hardly as often as it has been mentioned in the literature» (DU RIETZ 1949, p. 297, orig. Swed.). In the area the communities with bottom layer of *Drepanocladus revolvens* and *Campylium stellatum* play an important part. (*Drepanocladus revolvens* and *D. intermedius* are here united with the name of *D. revolvens*.) It is often difficult to distinguish two stages with *Drepanocladus revolvens* and *Campylium stellatum* as dominants. Often they occur as co-dominants. Other important bottom layer species are *Bryum pseudotriquetrum*, *Catocopium nigrum*, *Cinclidium stygium* and *Riccardia pinguis*. These bottom layer species are combined with a field layer of varying composition. Of species forming communities there might be mentioned *Carex dioeca*, *C. flava* and *C. atrofusca*. Among other important field layer species are *Angelica silvestris*, *Polygonum viviparum*, *Thalictrum alpinum*, *Carex panicea*, *Equisetum variegatum*, *Eriophorum latifolium*, *E. angustifolium*, *Festuca rubra* var. *mutica*, *Triglochin palustre*, *Selaginella Selaginoides*, *Viola biflora*, *Carex capillaris*, *Salix myrsinites*, *S. reticulata* and *Vaccinium uliginosum*. Communities with this composition of species are formed on rather strongly sloping ground with good drainage. *Scirpus*

*caespitosus* is lacking or occurs only as a solitary tuft. On places where the ground becomes less strongly sloping these communities change into *Scirpus caespitosus* - communities. These communities are totally dominated by *Scirpus caespitosus*, which forms dense mats. In the western parts of the area *Scirpus Hudsonianus* and *Nardus stricta* dominate in spots. In the *Scirpus caespitosus* - communities no very well delimited types can be distinguished. They imperceptibly change into each other from types rich in species through types less rich in species to types poor in species. As the communities mentioned above are situated on a strongly sloping ground the variations in the height of the water become very small. In the *Scirpus caespitosus* - communities which are situated on a less sloping ground, on the other hand, the hydrographic conditions are very varying from place to place. When the snow melts they are under water for a shorter or longer time owing to differences in the water flowing to and from at different places. In summer certain types can be very dry. Most of the field layer species listed above are represented in the *Scirpus caespitosus* - mat rich in species. In the types less rich in species such species as *Carex flava*, *C. panicea*, *C. capitata* and *Eriophorum latifolium* are lacking. Important components of these are *Triglochin palustre*, *Thalictrum alpinum*, *Andromeda Polifolia*, *Viola epipsila*, *Selaginella Selaginoides* and *Potentilla palustris*. Sometimes *Carex rostrata* can characterize large areas. In the bottom layer there are *Drepanocladus revolvens*, *Campylium stellatum*, *Cinclidium stygium* and *Riccardia pinguis*.

In DU RIETZ' arrangement according to the changes of wetness the driest parts consist of a *Tomenthypnetum*-association (-union). This type of community is well developed and very common in the whole area. The bottom layer is dominated by *Tomenthypnum nitens* and *Sphagnum Warnstorffianum*. Other important species are *Paludella squarrosa*, *Aulacomnium palustre*, *Bryum pseudotriquetrum* and *Mnium rugicum*. The field layer consists in general of the same species as the communities mentioned above; the species demanding greater wetness, however, disappear. Several meadow species take their place: *Gymnadenia conopsea*, *Orchis maculata*, *Rhinantus minor* ssp. *groenlandicus* and *Geranium silvaticum*. This type of community is easily delimited by its swelling mats, vigorously resplendent in red and yellow.

A further stage can follow. It consists of hummocks or hummock banks of *Sphagnum fuscum*. The bottom layer has a pure bog character, but in the field layer there often occur fen species, which have their



roots in the fen layer lying below. DU RIETZ wants to regard these formations as well as on the whole the miniature bogs of the mixed mires as a *Fuscetum*-association within that fen alliance where they are situated.

Spring communities of different types are well developed and play an important part in the area. These communities stand apart from the above mentioned series in the rich fens, arranged according to the composition of the bottom layer. In the spring communities the bottom layer is dominated by *Cratoneurum* and *Philonotis* species. *Drepanocladus revolvens* and *Campylium stellatum* play a subordinate part. Most of the field layer species are common with those occurring in the communities described above. Here might be mentioned among the most important ones: *Saussurea alpina*, *Thalictrum alpinum*, *Polygonum viviparum*, *Carex vaginata*, *Viola biflora*, *Equisetum variegatum* and *Pinguicula alpina*. Several new ones may be added: *Saxifraga aizoides*, *Crepis paludosa*, *Deschampsia caespitosa*, *Epilobium* species, *Poa alpina*, *Cystopteris montana*, *Tussilago farfara* and *Angelica Archangelica*.

## Forests with a field layer dominated by high-grown ferns.

(By HANS RUNEMARK.)

Among altiherbaceous meadows, more precisely among the alliance *Mulgedion alpini*, which is eutrophic and rich in species, NORDHAGEN also counts communities with dominance of high-grown ferns.

NORDHAGEN (1943) describes five different associations of this alliance with dominating fern vegetation.

1. *Mulgedio-Athyrietum filix-feminae*. This association lacks shrubs and trees.
2. *Betuletum mulgedio-athyriosum*. With a tree layer of *Betula*, and *Athyrium* dominating the field layer.
3. *Betuletum struthiopteris subalpinum*. With a tree layer of *Betula*, and *Matteuccia Struthiopteris* dominating the field layer.
4. *Alnetum struthiopteris subarcticum*. With a tree layer of *Alnus incana*, and *Matteuccia* dominating the field layer.
5. *Piceetum mulgedio-athyriosum*. With a tree layer of *Picea abies*.

Of these 2, 3 and 4 occur on the northern side of Torneträsk. As at least in this area transitional types between the different associations are common and as for the rest they are little differentiated they will here be treated as a unity with the name of »fern forests».

The fern forests form narrow stripes often on rather strongly sloping ground in the valleys of brooks and along rills in the most eutrophic parts of the area. They are rather common on the northern side of Torneträsk (see Fig. 2) and are exceptionally richly developed. *Matteuccia* reaches generally a height of more than 1.5 metres and the whole vegetation makes an impression of almost southern luxuriance. The reasons of this rich development are probably to find in the calciferous easily weathering schists, which form the bedrock, in the rich precipitation and also in the southern exposure of the district.

The tree layer, which is generally very well developed, usually consists of *Alnus incana* and solitary specimens of *Betula tortuosa*, *Prunus Padus* and *Sorbus aucuparia*. In other cases *Betula tortuosa* alone forms the tree layer. In the field layer *Matteuccia Struthiopteris* or *Athyrium Filix-femina* dominate alone or sometimes together with *Dryopteris Filix-mas* and *austriaca*. Of other species none generally reaches a higher degree of covering than 1 according to the HULT-SERNANDER scale, possibly with the exception of *Stellaria nemorum* ssp. *montana*. The light conditions at the ground are very bad, and a bottom layer is almost wholly lacking. In spots one finds some moss, usually *Brachythecium reflexum*, for the rest the ground is covered by withered fern leaves.

Preference species for the fern forests of the district are beside *Matteuccia*, *Corydalis fabacea* (which occurs only at some neighbouring localities below Pesisvare; new to Torne Lappmark), *Urtica gracilis* and *Actaea* cf. *erythrocarpa*. The last two species also sometimes occur in meadow communities in southern precipices.

The fern forests show a very small variation. They might, however, be divided into a *Matteuccia* type and an *Athyrium* type.

The following list shows the constant percentage for the species from a number of investigated localities. Square analyses have not been made, but as the fern forests generally cover only small areas and no continuous transitions to other communities occur the lists from the localities can be considered as approximately corresponding to analyses of 100 m<sup>2</sup> squares.

Species	1.	2.	Species	1.	2.
<i>Alnus incana</i> .....	60	80	<i>Geum rivale</i> .....	70	60
<i>Betula tortuosa</i> .....	80	40	<i>Lactuca alpina</i> .....	100	100
<i>Prunus Padus</i> .....	70	20	<i>Matteuccia Struthiopteris</i> ..	100	—
<i>Sorbus aucuparia</i> .....	30	40	<i>Melampyrum silvaticum</i> ...	80	60
<i>Ribes spicatum</i> ssp. <i>lapponicum</i> .....	70	20	<i>Melandrium rubrum</i> .....	30	20
<i>Actaea</i> cf. <i>erythrocarpa</i> ...	30	—	<i>Melica nutans</i> .....	10	20
<i>Agropyron caninum</i> .....	20	20	<i>Milium effusum</i> .....	60	80
<i>Angelica Archangelica</i> .....	10	40	<i>Myosotis silvatica</i> ssp. <i>frigida</i>	50	20
— <i>silvestris</i> .....	10	—	<i>Paris quadrifolia</i> .....	90	80
<i>Anthriscus silvestris</i> .....	70	80	<i>Poa nemoralis</i> .....	20	—
<i>Athyrium Filix-femina</i> .....	40	100	<i>Polygonatum verticillatum</i> ..	20	—
<i>Calamagrostis purpurea</i> ....	—	20	<i>Ranunculus acris</i> .....	—	20
<i>Caltha palustris</i> .....	30	—	<i>Rubus idaeus</i> .....	70	60
<i>Carex norvegica</i> .....	10	—	<i>Rumex acetosa</i> ssp. <i>lapponica</i> .....	60	100
<i>Cerastium fontanum</i> ssp. <i>scandicum</i> .....	—	20	<i>Salix caprea</i> ssp. <i>borealis</i>	10	—
<i>Cirsium heterophyllum</i> ....	20	20	<i>Saussurea alpina</i> .....	—	20
<i>Corydalis fabacea</i> .....	10	20	<i>Stellaria nemorum</i> ssp. <i>montanum</i> .....	100	100
<i>Crepis paludosa</i> .....	10	—	<i>Solidago Virgaurea</i> .....	—	20
<i>Cystopteris montana</i> .....	20	20	<i>Trientalis europaea</i> .....	—	60
<i>Dryopteris austriaca</i> .....	60	40	<i>Trollius europaeus</i> .....	20	40
— <i>Filix-mas</i> .....	10	20	<i>Tussilago farfara</i> .....	10	—
<i>Dryopteris phegopteris</i> ....	10	80	<i>Urtica gracilis</i> .....	80	—
<i>Epilobium palustre</i> .....	—	20	<i>Valeriana sambucifolia</i> ....	90	100
<i>Filipendula Ulmaria</i> .....	50	40	<i>Viola biflora</i> .....	70	100
<i>Geranium silvaticum</i> .....	20	60			

1. 10 investigated localities with dominance of *Matteuccia*.

2. 5 investigated localities with dominance of *Athyrium Filix-femina*.

These subalpine fern forests on the whole reach their richest development in N. Norway in Nordland, Troms and Finnmark (NORDHAGEN 1943). In Sweden they find their way through the low passes into the large west-eastern valleys in the mountain range, as offshoots from the large Norwegian area. In Sweden they occur from S. Jämtland up to Torne Lappmark. They are evidently strongly favoured by oceanic climate. In the Torneträsk district *e.g.* there occur no fern forests to the east of Maivatjåkko (=Vaivantjåkko). In Sweden, with the exception of the Torneträsk area, they are represented by a rather poor type (TENGWALL, 1920, H. SMITH, 1920). In solitary localities rather rich types are, however, to be found. Thus in 1949 in N. Jämtland at Jormlien I saw a fern forest below a southern precipice. The tree layer was formed by *Alnus incana*, the field layer was

dominated by *Athyrium Filix-femina*. Other species were *Lactuca alpina*, *Stellaria nemorum* ssp. *montana*, *Stachys silvatica*, *Milium effusum*, *Rumex acetosa* ssp. *lapponicus*, *Aconitum septentrionale*, *Trientalis*, *Calamagrostis purpurea*, *Viola biflora* and *Polygonatum verticillatum*.

In the Petsamo district in N. Finland, too, fern forests occur with *Athyrium Filix-femina* as the dominating fern, but for the rest with common and uninteresting species (KALELA, 1939).

## The vegetation on precipices with a southern exposure ("southern precipices").

(By HANS RUNEMARK.)

The whole of regio subalpina on the northern side of Torneträsk is strongly exposed to the south. In the area there also occur precipices towards the south. The whole area gets through its exposure a stronger insolation and a higher total sum of warmth than the surrounding parts. The strongest effect is of course attained in the southern precipices. FRÖDIN (1915) has made measurements of the temperature during a period of a month in July—August of a southern precipice in Lule Lappmark. He observed that the temperature of the uppermost part of the boulder land in the southern precipice 1.6 metres over the ground was on the average 1.7° C. higher than in an adjacent comparable locality on horizontal ground on days with fine weather. It might be supposed that the difference of temperature is considerably greater closer to the ground. The effect of southern exposure becomes incomparably stronger in a continental district with a small cloud covering and a small frequency of mists, than in an oceanic district. Southern precipices in the mountain districts of Sweden are thus much more influenced by a southern exposure than similar localities in Norwegian coastal districts.

The vegetation of regio subalpina on the northern side of Torneträsk is on the whole influenced by the southern exposure of the district. The generally strong declivity brings with it beside an increased insolation also a more vigorous drainage of precipitation and as at the same time the evaporation is strong the soaking process in the upper layers of the ground is delayed. — The birch forest is extremely well developed. The whole vegetation shows a luxuriance uncommon to





Fig. 3. Sketch of a southern precipice. — 1. The rock wall with a shelf. 2. The weathering gravel border. 3. The boulder land.

regio subalpina. Several species which are otherwise rare in regio subalpina are more or less common here, *e.g.* *Rubus idaeus*, *Valeriana sambucifolia*, *Polygonatum verticillatum*, *Paris quadrifolia*, *Prunus Padus*, *Dryopteris phegopteris* and *Polystichum Lonchitis*. Other factors play a part, too, *e.g.* the oceanic tendency of the climate in the western part of the area and the calciferous, easily weathering bedrock.

The strongest effect of the southern exposure on the flora is found in the pure southern precipices. Here there occur a number of species which are lacking in other localities in Torne Lappmark, generally lowland plants with a more or less southern tendency in their distribution. The distribution of these plants in Norrland has been given a thorough investigation by ANDERSSON and BIRGER (1912).

The communities on and around the southern precipices form a mosaic and are often more or less fragmentary, which is due to the highly changing edaphic and micro-climatic factors. Among those which have the greatest importance there might be mentioned the lime content, the weathering conditions of the mineral, the watering and the shading.

The southern precipices most rich in species are the big dolomite precipices on Ortovare and Lulletjärro. Here there occur practically the whole of the southern element and three species are wholly limited to these localities, *viz.* *Thelypteris Robertiana*, *Cypripedium Calceolus* and *Epipactis atropurpurea*. Also southern precipices where the rocks are formed by easily weathering calciferous schists have a rich southern element. Strongly contrasted to these are the poorly calciferous hard

schist and Archaean rock precipices which generally have a poor flora, and the only species with a southern tendency to be found here are *Sedum annuum* and *Woodsia ilvensis*. Among the reasons of this which might be mentioned are the very bad watering, the difficultly weathering minerals and the low calciferosity. The last factor is of a special great importance as the southern species here in their northern outposts have considerably larger demands than elsewhere in their areas with regard to the lime content of the substratum.

Most southern species are more or less strictly bound to a certain type of vegetation. Thus there occur an element bound to the rocks exposed to sun, a meadow element which demands shading, and an element bound to the weathering gravel immediately below the rock wall.

The rock element is bound to the precipice itself with its rock shelves and to a certain extent to the boulder land below the precipice. Among southern species occurring in such localities in our area may be mentioned *Epilobium collinum*, *Asplenium Ruta-muraria* (one locality in the precipice of Lulletjärro and another in a small schist precipice to the east of Jebrenjokk; new to Torne Lappmark), *Sedum annuum* and *Polypodium vulgare* and beside *Lappula deflexa*, which cannot, however, be counted as a southern species, as in Scandinavia it is practically wholly restricted to precipices, and is found only in one locality in southern Sweden. In its total distribution it is circumpolar.

To the rock element of southern precipices one may also count some alpine species e.g. *Draba hirta*, *Asplenium viride* and *Saxifraga groenlandica*. Of the reasons for the appearance of such species we know very little. One factor to be pointed out is the weak competition.

Among the rock species there occurs also, though weakly represented, a continental element. The species that belong here are *Draba nemorosa*, *Satureja acinos*, *Potentilla multifida* and probably the lichen *Rhizocarpon chionophiloides*. These species are rare and the only one occurring in the Torneträsk district is *Rhizocarpon chionophiloides*, which has a locality on the boulder land at a schist precipice below Ortovare, besides it has a similar locality in Västerbotten (new to Sweden) and a few Finnish localities. It is in its total distribution (arctically?) eurosibiric. The other species usually occur on rock shelves on the very precipice, *Satureja* mainly along the coast of Norrland up to Älvsby in Norrbotten, *Potentilla multifida* and *Draba nemorosa* on a few southern precipices in the easternmost part of the mountain range in Lapland. The occurrence of these species on rock shelves

and sun-exposed boulder land in southern precipices has surely a connection with the continental micro-climate which prevails here, with a low humidity and great temperature differences.

DEGELIUS (1945) has shown another rock element of a totally opposite type. On large boulders shaded by trees, situated in the lowest part of the boulder land and below that, there occur a number of species of an oceanic type. Of such species favoured by oceanic climate there occur below the precipices of Ortovare *e.g.* the lichens *Parmeliella plumbea*, *Peltigera scutata* and some *Pannaria* species. From a southern precipice in Lule Lappmark DEGELIUS also mentions *Pannaria pityrea* and *Dendriticocaulon umhausiense*. Among reasons for the occurrence here of these species, besides the relatively high humidity, the comparatively high temperature is worth mentioning. »For the oceanic species are in general not only demanding moisture but also warmth» (DEGELIUS; transl. from the Swedish). A thorough investigation of the cryptogam flora would surely increase our knowledge of the part played by the different geographical elements in the rock flora, and in the flora of southern precipices in general.

On the narrow stripe of weathering gravel that is generally found immediately below the precipice itself and below which the boulder land begins, there occur a rather large number of southern species. This is however only the case, if there is a relatively satisfactory supply of water, otherwise vigorous specimens of *Juniperus communis* dominate and other vegetation is almost lacking. On weathering gravel we find southern species as *e.g.* *Fragaria vesca*, *Silene rupestris*, *Anthyllis vulneraria* var. *lapponica*, *Erysimum hieraciifolium*, *Arabis hirsuta*, *Viola rupestris*, *Epipactis atropurpurea* and *Thelypteris Robertiana*. Among other species common here may be mentioned *Melica nutans*, *Stellaria graminea*, *Erigeron acre* ssp. *politum* and *Saxifraga adscendens* (which is rare in Torne Lappmark and mainly bound to southern precipices on the forest limit and the lowest part of regio alpina). On these strongly sloping stripes of weathering gravel, to a large extent lacking a bottom layer, there are seldom formed closed communities, probably on account of the great mobility of the substratum. Factors favourable to the southern species are besides the high temperature, the high percentage of mineral salts of the weathering gravel and the lack of competition.

Where rills and brooks flow down on southern precipices or where the earth layers are comparatively immobile, there occur closed meadow communities. There generally occurs a tree layer of *Sorbus aucuparia*, *Prunus Padus* or solitary birches. On a few precipices to the east of

Ortojokk where water filters down along the whole precipice there are formed extraordinarily luxuriant altiherbaceous meadows, generally dominated by *Lactuca alpina* and *Chamaenerium angustifolium*. Among southern species in shadowy meadow-like localities might be mentioned *Epilobium montanum*, *Veronica officinalis*, *Viola montana*, *Cypripedium Calceolus* and *Carex pallescens*.

The southern element of the southern precipices has with regard to its immigration history been thoroughly treated by ANDERSSON and BIRGER (1912). They have shown that the chief part of the southern species of our mountain districts in Lapland has immigrated from the west through the passes to Norway. Among species belonging to this group for instance *Viola rupestris*, *Sedum annuum*, *Asplenium Ruta muraria* and *Silene rupestris* may be mentioned. For some species found chiefly in the eastern part of the mountain range in Lapland, one must accept an immigration from the east or the south-east as they are lacking in northern Norway, e.g. *Actaea erythrocarpa*, *Potentilla argentea* and *multifida* and *Draba nemorosa*. Some species are nowadays so evenly spread that it is not possible to draw any conclusion from the map, this is true of e.g. *Fragaria vesca*.

Probably the colonization of the southern species has taken place during the postglacial warmth time when the southern element must have had a considerably wider distribution than now. This means that the southern precipices are refuges containing a southern relict flora. With regard to single species one cannot neglect the possibility of a long distance spread in recent time.

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## **Studies on chromosome numbers and certain meiotic features of several Finnish moss species.**

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### **Introduction.**

A survey of the reviews dealing with the results of cytogenetical research on the Bryophyta (WETTSTEIN, 1925; ALLEN, 1935, 1945; LOWRY, 1948) reveals that the amount of work done in this field during the last fifty years is considerable. We have, in this connection, only to remember that even the classical investigations of cytogenetics made by WETTSTEIN and his school, and HEITZ were carried out using Bryophyta as material.

If, however, we compare the extent of our knowledge of the cytogenetics of the Bryophyta with that of higher plants gained during the same period, we are obliged to state that the Bryophyta, especially the mosses, have remained, nevertheless, very much in the background. The causes of this are, of course, easy to understand. But in spite of the technical difficulties confronting cytogenetical investigations on the Bryophyta, it seems obvious that considerable opportunities may exist in this field of research. Besides the service thus rendered to Bryology there might arise a possibility of throwing light upon many more general problems of cytogenetics, taxonomy and evolution.

Our knowledge is very inadequate even as regards such a basic matter as the chromosome numbers of the Bryophyta and particularly those of mosses. The last chromosome list of mosses published by LOWRY (1948) reveals that only a small fraction of the chromosome numbers of the moss species are known.

The present study has aimed at reducing this lack. In the following pages will be presented the chromosome numbers of forty Finnish moss species. In an earlier paper the author has already published chromo-

some counts of five moss species belonging to the family *Grimmiaceae* (VAARAMA, 1949). As the chromosome counts made are based mainly on meiotic divisions in the sporophyte, some preliminary remarks on meiotic phenomena have also been included in this paper. A few papers dealing with this special matter will be published in the near future.

### Material and Methods.

The material has been collected during the year 1949 in the vicinity of the State Horticultural Institute, Piikkiö, southwestern Finland. The species investigated belong mainly to the most frequent and widely distributed species of the Finnish moss flora. The purpose of the study has been to find meiotic divisions in every species. In a few cases, however, the chromosome counts have been made from the mitoses in the young archesporial cells of the sporogone.

The aceto-orcein squash method only has been used in the making of preparations. This method has already earlier been observed (VAA-RAMA, 1949) to be suitable for moss material. The archesporial tissue joined with the columella has been squeezed out from a sporogone at a suitable stage of development, and immersed without pre-fixation in a drop of aceto-orcein. On applying suitable pressure for the unmacerated pieces of material the spore mother cells (SMC) orientate themselves neatly side by side under the cover glass forming a coherent group. The drawback of this method is the weak staining of the chromosomes in the innermost SMCs of the group which could, however, be avoided by previous maceration of the pieces.

The preparations have been examined, as far as possible, in a fresh condition. The making permanent of the preparations was effected by separating the cover glass in 70 per cent alcohol and then mounting in Euparal.

The counting of chromosome numbers from meiotic metaphases of the mosses is difficult insofar as to get reliable results it is necessary to have numerous divisions and a certain experience in observation. For it is rather characteristic of the heterotypic division in the mosses that the anaphase separation of the chromosomes begins unevenly in individual chromosomes. There are thus often difficulties in the determination of the exact chromosome number owing to the precociously divided bivalents.

A great part of the material studied has been checked as to deter-

minations by Doctors HERMAN PERSSON, Stockholm, Sweden, and R. TUOMIKOSKI, Helsinki, Finland. I wish, in this connection, to express my cordial thanks for the courtesy of both these gentlemen. As to nomenclature the author has followed JENSEN's (1939) manual of Fennoscandian mosses. The observations that follow have been arranged according to the order of families and genera given in this work.

The terms tetraploid, hexaploid etc. for polyploid forms of mosses have been used in the following text. This terminology has been based on the sporophytic chromosome numbers of the forms in question. The terms bivalent and tetravalent as used earlier by E. and E. MARCHAL (1911) and WETTSTEIN (1924 a) for induced tetra- and octoploid races are a little confusing. The application of terminology to Bryology consistent with higher plants will certainly be advantageous.

### Observations.

*Polytrichaceae.* Three species of the family have been examined, viz. *Polytrichum piliferum* HEDW. (Fig. 1 a), *P. juniperinum* HEDW. (Fig. 1 b) and *P. commune* HEDW. (Fig. 1 c). The chromosome number of the two first-mentioned species,  $2n=14$ , has been counted from the mitoses of young archesporial cells. The chromosome number of the last-mentioned species,  $n=7$ , has been observed from the heterotypic metaphase. The chromosome numbers of all three species were known earlier. J. and W. LEEUWEN-RIJNVAAN (1907, 1908) and VANDENDRIES (1912) report the chromosome number  $n=6$  in *P. piliferum*. The chromosome number of *P. juniperinum* is according to J. and W. LEEUWEN-RIJNVAAN (1907, 1908), ARENS (1907), ALLEN (1912) and VANDENDRIES (1912)  $n=6$ . HEITZ (1928) gives the number  $n=(6-7)$  and KURITA (1937)  $n=7$ . Similarly the number in *P. commune* is according to the older investigators  $n=6$ . All the recent counts are identical with the present count  $n=7$  (HEITZ, 1928; JACHIMSKY, 1935 and KURITA, 1937).

The prevailing basic number of the genus seems to be seven (cf. LOWRY, 1948). In spite of the fact that numerous older counts have given the result  $n=6$  it is very probable that this is not due to different chromosome races but rather to erroneous counts. The chromosome number  $n=14$  reported by KURITA (1937) indicates, however, that polyploid races may be found within the genus.

*Bartramiaceae.* Two species of the genus *Bartramia* have been studied. These were *B. pomiformis* var. *crispa* (WEB. & MOHR) BR. &



SCH. (Fig. 1 *d*),  $n=8$ ; *B. ityphylla* BRID. (Figs 1 *e* and *f*),  $n=12$ . There can be found in the literature earlier chromosome counts in *B. pomiformis*. HEITZ (1928) reports from Germany the number  $n=7-8$ , KURITA (1937), again, from Japan the number  $n=8$ . The assumption that the basic chromosome number of the genus may be  $x=4$  has been warranted by the observation of the chromosome number  $n=12$  in *B. ityphylla*. In this case *B. pomiformis* would be a tetraploid and *B. ityphylla* a hexaploid species. In *B. ityphylla*, the chromosomes of which are clearly larger than those in *B. pomiformis*, there have been observed a few SMCs each containing a single tetravalent chromosome association (Fig. 1 *f*).

*Aulacomniaceae*. From this family only one species, *Aulacomnium palustre* (HEDW.) SCHWAEGR., has been examined. Its chromosome number was  $n=12$  (Fig. 1 *g*), thus differing from the earlier count,  $n=(9-10)$ , of HEITZ (1928).

*Mniaceae*. Three species belonging to the cytologically best known moss genus *Mnium* have been examined, viz. *M. medium* Br. eur. (Fig. 1 *j*),  $n=12$ ; *M. punctatum* HEDW. (Fig. 1 *i*),  $n=7$  and *M. pseudopunctatum* BR. & SCH. (Fig. 1 *h*),  $n=13$ . The chromosome numbers of all three species were known earlier. LOWRY (1948) reports for *M. medium* the chromosome number  $n=12$  from the United States. All the chromosome numbers of *M. punctatum* to be found in the literature correspond to the number established from the Finnish material (HEITZ, 1928, 1942; JACHIMSKY, 1935; LOWRY, 1948). The chromosome number of *M. pseudopunctatum* determined by HEITZ (1942) is the same as that obtained from Finnish material. LOWRY (1948), on the contrary, reports the count,  $n=14$ , from American material. According to the oral communication given by Dr. R. TUOMIKOSKI the American *M. pseudopunctatum* has certain morphological dissimilarities as compared with the European type and may thus be considered as a parallel species (*M. Andrewsianum* STEERE ?). The established chromosome number,  $n=13$ , supports this opinion, indicating that the European form differs from the American one also as regards the chromosome number.

When comparing the chromosome morphology of *M. punctatum* and *M. pseudopunctatum*, both originating from the United States, LOWRY (1948, p. 36) draws the conclusion that the latter species is an autotetraploid derived from *M. punctatum*. HEITZ (1942), on the con-



Fig. 1. — *a* *Polytrichum piliferum*. A mitotic metaphase from a young archespore cell.  $2n=14$ . — *b* *P. juniperinum*. As above.  $2n=14$ . — *c* *P. commune*. Heterotypic metaphase.  $n=7$ . — *d* *Bartramia pomiformis* var. *crispa*.  $n=8$ . — *e* *B. ityphylla*.  $n=12$ . — *f* *B. ityphylla*. A tetraivalent chromosome association can be seen on the left. — *g* *Aulacomnium palustre*.  $n=12$ . — *h* *Mnium pseudopunctatum*.  $n=13$ . — *i* *M. punctatum*.  $n=7$ . The »m»-bivalent divided precociously. — *j* *M. medium*.  $n=12$ . Observe the localized chiasmata. — *k* *Funaria hygrometrica*.  $n=28$ . — *l* *Pottia truncata*.  $n=25$ . — All the preparations made using the aceto-orcein squash method.  $\times 2300$ .

trary, has established only one small »m»-chromosome, very characteristic of *M. punctatum*, in the idiogram of the European *M. pseudopunctatum*. This has led him to draw the conclusion that *M. pseudopunctatum* is an amphiploid originating from hybridization between *M. punctatum* and some *Mnium* species provided with six gametophytic chromosomes. The first meiotic division of *M. pseudopunctatum*, depicted in Fig. 1 h, as compared with that of *M. punctatum* (Fig. 1 i) does not show such a well-defined »m»-chromosome as can be seen in *M. punctatum*. The present author has observed in *Ptilium crista castrensis* (VAARAMA, unpubl.) that a totally heterochromatic bivalent, peculiar in its mode of origin and called in this paper the »special» bivalent (cf. p. 250), occurring normally in the meiosis of the diploid sporophyte is to be seen joined with its homologue in the meiosis of the occasionally arising tetraploid sporophytes. In endeavouring to explain the origin of *M. pseudopunctatum* the presence of a corresponding phenomenon as regards the »m»-chromosome cannot be ignored. As a matter of fact, the »m»-chromosomes are heterochromatic members of the XY-system of the species (JACHIMSKY, 1935). On the other hand, in the resting nuclei of the *M. pseudopunctatum* gametophyte can be found only two heteropycnotic bodies. This fact, together with the observed great size of the heterochromatic bivalent in *M. pseudopunctatum* support the assumption that the fusion of »m»-chromosomes has occurred. Whether *M. pseudopunctatum* is an autoploid or an amphiploid cannot be decided without further investigation. At any rate, it seems possible that a form with 13 chromosomes may arise from forms having 7 chromosomes.

*Funariaceae.* Only one species, *Funaria hygrometrica* HEDW., has been examined (Fig. 1 k). The chromosome number observed was  $n=28$ . The species is one of those used by WETTSTEIN in his famous experiments. The chromosome numbers counted from WETTSTEIN's material collected in nature have been without exception  $n=14$  (WETTSTEIN, 1923, 1924 a). The tetraploid ( $n=28$ ) form named by WETTSTEIN *F. hygrometrica* var. *bivalens* has been obtained experimentally by regenerating the tissues of the sporophyte (WETTSTEIN, 1924 b). The present material reveals, however, that corresponding polyploid races can also occur in natural habitats. Whether any morphological differences can be found between the natural diploid and tetraploid races of the species has not been investigated for the present. The range of the tetraploid race is also so far unknown.

**Pottiaceae.** From the species belonging to this family there have been examined: *Pottia truncata* (HEDW.) FÜRN. (Fig. 1 l),  $n=25$ ; *Weisia controversa* HEDW. (Figs 2 a and b),  $n=14$  and *Barbula unguiculata* HEDW. (Fig. 2 c),  $n=13$ . Only the last mentioned species has been previously known cytologically in that JACHIMSKY (1935) has published a figure showing the heterotypic metaphase of the species. In it can be seen 13 bivalents. One bivalent, as in the present material, is larger than the others. It is probably also heteropycnotic. The shape of the bivalent is, however, quite symmetrical.

*Pottia truncata* has very small chromosomes and it obviously represents a high degree of polyploidy.

In the meiosis of *Weisia controversa* features of particular interest can be observed. As can be seen in Fig. 2 a the bivalents in the heterotypic division appear to be rather peculiar. Each bivalent seems to be composed of two parallel co-orientated bivalents. In most cases all connections between them seem to be totally lacking. At anaphase (Fig. 2 b) a closer connection between the halves of the separating chromosomes seems, however, to exist. The complete picture of the course of meiosis is for the present lacking owing to the scarcity of the material. The drawing of any conclusions has, therefore, been omitted. There may be, however, reason in this connection to mention that SCHRADER (1940) has described in a hemipterous insect *Rhytidolomia senilis* bivalents resembling to a great extent those of *Weisia controversa*.

**Dicranaceae.** Chromosome counts have been made of the following species: *Paraleucobryum longifolium* (HEDW.) LOESKE (Fig. 2 d),  $n=12$ ; *Dicranum spurium* HEDW. (Fig. 2 e),  $2n=24$ ; *D. undulatum* Br. eur. (Fig. 2 f),  $n=12$ ; *D. scoparium* HEDW. (Fig. 2 g),  $n=12$ ; *D. majus* TURN.,  $n=12+5$  accessory chromosomes; *Cynodontium strumiferum* (HEDW.) DNot. (Fig. 2 h),  $n=15$ ; *Amphidium lapponicum* (HEDW.) SCHIMP. (Fig. 2 i),  $n=16$  and *Ceratodon purpureus* (HEDW.) BRID.,  $n=13$ ,  $2n=26$ .

The chromosomes of *Paraleucobryum* seem to resemble in size and number those of the *Dicranum* species. Characteristic of the species is a large 3-segmented bivalent which is probably partly heterochromatic. In the genus *Dicranum* the chromosome number  $n=12$  seems to prevail as far as can at present be judged. SHIMOTOMAI and KOYAMA (1932) report, however, the chromosome number  $n=11$  in the species *D. japonicum*. HEITZ (1928) has observed the chromosome



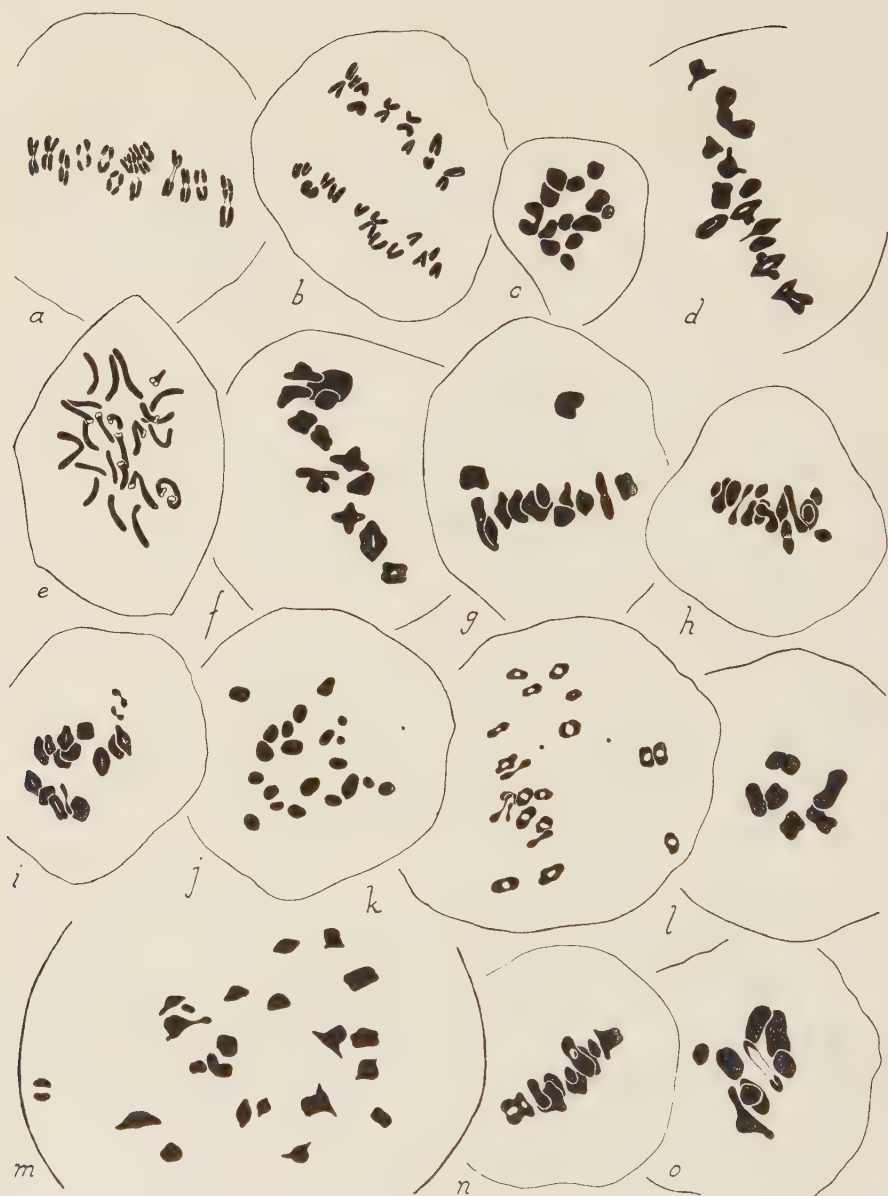


Fig. 2. — *a* *Weisia controversa*. Heterotypic metaphase.  $n=14$ . Observe the separate halves of the bivalents. — *b* *W. controversa*. Heterotypic anaphase. — *c* *Barbula unguicula*.  $n=13$ . — *d* *Paraleucobryum longifolium*.  $n=12$ . — *e* *Dicranum spurium*. Archesporial mitosis.  $2n=24$ . — *f* *D. undulatum*.  $n=12$ . — *g* *D. scoparium*.  $n=12$ . Both the chromosomes to be seen above the plate belong to the largest bivalent

number  $n=10-12$  in two species also included among the objects of the present investigation, viz. *D. undulatum* and *D. scoparium*. The meiotic chromosome complement of the genus *Dicranum* is characterized by a large heteropycnotic bivalent which can occasionally be seen divided precociously, as in the Fig. 2 g.

A particularly interesting feature is the presence of the five heterochromatic accessory chromosomes in the *D. majus* population investigated. These can be considered from their mode of conjugation to be isochromosomes. A more detailed description of them will be published elsewhere (VAARAMA, 1950).

Characteristic of the chromosome complement of *Amphidium lapponicum* are the three »m»-chromosomes, which are clearly smaller than the other chromosomes of the species (Fig. 2 i).

*Ceratodon purpureus* has also been the object of several earlier investigations. The most recent chromosome numbers reported are in accordance with the number presented in this paper (JACHIMSKY, 1935; SHIMOTOMAI and KIMURA, 1936). HEITZ (1928) has reported the chromosome number  $n=11-12$ .

**Orthotrichaceae.** The species examined and the chromosome numbers found are as follows: *Ulota curvifolia* (VG.) BRID. (Figs 2 j and k),  $n=21+2$  accessory chromosomes, and *Orthotrichum speciosum* NEES. (Fig. 2 l),  $n=6$ . No one of the species belonging to this family has been investigated earlier.

*Ulota curvifolia* is the third moss species in which the author has been able to find accessory chromosomes. The accessories of *Ulota* closely resemble those found earlier in the species *Grimmia trichophylla* var. *Mühlenbeckii* (SCHIMP.) HUSN. (= *G. Mühlenbeckii* SCHIMP.) of the family *Grimmiaceae* (VAARAMA, 1949). The accessories in *Dicranum majus* deviate in certain respects from those now in question (VAARAMA, 1950). The accessories in *Grimmia* and *Ulota* are fragmen-

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divided precociously. — h *Cynodontium strumiferum*,  $n=15$ . — i *Amphidium lapponicum*,  $n=16$ . Observe the 3 »m»-chromosomes. — j *Ulota curvifolia*,  $n=21+$  at the right hand one small bivalent formed by two accessory chromosomes. — k *U. curvifolia*. The accessories have remained as univalents. — l *Orthotrichum speciosum*,  $n=6$ . — m *Hedwigia ciliata*,  $n=22$ . The leftmost chromosome pair shows distance conjugation. — n *Dichelyma falcatum*,  $n=10$ . Observe the large asymmetrical bivalent. — o *Brachythecium albicans*,  $n=9$ . Observe the ring-shaped »special» bivalent. — All the preparations made using the aceto-orcein squash method.  $\times 2300$ .

tarily small and heterochromatic (Figs 2 *j* and *k*) but despite this frequently capable of conjugating with one another. Sometimes they remain as univalents (Fig. 2 *k*). In addition, characteristic of the accessory chromosomes is their frequently lacking ability to congregate normally at metaphase. They accordingly often lie outside the metaphase plate (Fig. 2 *j*).

*Ulota curvifolia* obviously represents a high degree of polyploidy within the family. If we consider seven as the basic chromosome number in the genus, the species is consequently a hexaploid. This assumption is supported by the low chromosome number,  $n=6$ , established in *Orthotrichum speciosum*.

**Hedwigiaceae.** The only Finnish representative of the family, *Hedwigia ciliata* (HEDW.) BR. & SCH., has been examined. The meiotic bivalent number found was  $n=22$  (Fig. 2 *m*).

In the meiosis of the species a rather peculiar phenomenon has been observed. 21 of the bivalents behave normally during the course of the heterotypic division. One chromosome pair, however, wholly deviates from the others (the leftmost pair in Fig. 2 *m*) in that the members of the pair never conjugate normally with one another. They nevertheless behave as a pair. The distance between them is, however, considerable and no visible connective between them has been observed.

LORBEER (1934) has described a similar phenomenon in several liverwort species and he calls this mode of pairing *distance conjugation*. It is intended to examine the phenomenon, which will have importance in interpretation of the forces of the internal mechanics of meiosis, more carefully.

**Fontinalaceae.** One species, *Dichelyma falcatum* (HEDW.) MYR., has been examined. The chromosome number determined was  $n=10$  (Fig. 2 *n*). Among the species belonging to the family only *Fontinalis antipyretica* has been investigated earlier by HEITZ (1926, 1928). He reports the chromosome number  $n=8$ . In Fig. 26 among the bivalents there can be distinguished one large asymmetrical body which probably represents the sex-chromosome system.

**Brachytheciaceae.** All the species examined belong to the genus *Brachythecium*. The species and their chromosome numbers are as follows: *B. albicans* (HEDW.) BR. & SCH. (Fig. 2 *o*),  $n=9$ ; *B. salebrosum* (WEB. & MOHR) BR. & SCH. (Fig. 3 *a*),  $n=13$ ; *B. Starkei* ssp. *curtum*

(LINDB.) C. JENS. (Fig. 3 b),  $n=20$ ; *B. velutinum* (HEDW.) BR. & SCH. (Fig. 3 c),  $n=11$  and *B. populeum* (HEDW.) BR. & SCH. (Figs 3 d and e),  $n=10$  and  $n=9$ . In the literature can be found only the chromosome number for *B. velutinum*,  $n=10$  (E. and E. MARCHAL, 1911), which differs from that presented above.

The fixability of the chromosomes of all the *Brachythecium* species using the aceto-orcein method seems to be rather poor. The matrix of the chromosomes appears to be less firm than usual, the sticking together of the bivalents being thus a common phenomenon. The exact determination of the chromosome number is, therefore, more difficult than usual.

The common occurrence of aneuploidy in the genus *Brachythecium* is indicated by the chromosome numbers established. It seems that 9 and 10 are the prevailing basic chromosome numbers and, in addition, there exist different kinds of aneuploid modifications of the numbers mentioned (*B. salebrosum*, *B. velutinum*). The chromosome number established for *B. Starkei* ssp. *curtum*, on the other hand, reveals that polyploidy can also be found in the genus.

The different chromosome numbers met with in *B. populeum* reveal the presence of intraspecific chromosome races in the genus. The populations in which the different chromosome numbers were detected were growing on rather different habitats. The form provided with 10 chromosomes grew on a stone in a fairly dense and shady spruce-forest of the *Myrtillus* type. The form with 9 chromosomes, on the contrary, grew on a vertical concrete-block wall of a glass-house. The former form represents a mesophilous type with relatively long shoots and deep green colour, the latter, on the other hand, a xerophilous type with short shoots of a pale green colour. Both the forms, which can best be considered as two different ecotypes of the species, seem also to have genotypical differences expressing themselves not only in the chromosome number but also in the morphology of the chromosomes. A small bivalent lacking in the form with 9 chromosomes can be found in the form provided with 10 chromosomes. In addition, there are structural differences between the ring-shaped heterochromatic »special» bivalents occurring in both of the forms (Figs 3 d and e). This bivalent is relatively small and symmetrical in the mesophilous ecotype whereas it is considerably larger and asymmetrical in the xerophilous one.

The »special» bivalent mentioned above represents a peculiar chromosome type up to the present found only among the pleurocarpic



mosses. Its development is rather exceptional and so far unknown in the plant kingdom. In the genus *Brachythecium* such a bivalent can also be found in *B. albicans* (Fig. 2 o). The bivalent is obviously totally heterochromatic and appears at the meiotic prophase on the surface of a body resembling a nucleolus. It is heteropyncotic as compared with the other chromosomes. The »special» bivalent congregates normally in the metaphase plate. The nucleolus-like body has by that time disappeared. It is very questionable if there exist any real chiasmata between the halves of the »special» bivalent. The anaphase separation of the bivalent halves is normal. According to an oral communication by Professor ESKO SUOMALAINEN there is found in the animal kingdom a case corresponding to that described above (SUOMALAINEN, unpubl.). In the weevils belonging to the genus *Otiorhynchus* the heterochromatic sex-chromosome system of XY-type arises in a practically similar way. A more detailed description of this bivalent type will be published in another paper (cf. also pp. 244 and 252).

*Amblystegiaceae.* The species of this family examined and their chromosome numbers are as follows: *Drepanocladus uncinnatus* (HEDW.) WARNST. (Fig. 3 f),  $n=12$  and *Amblystegium serpens* (HEDW.) BR. & SCH. (Fig. 3 g),  $n=22$ . The chromosome number  $n=12$  of the latter species was previously known from material determined in Central Europe (E. and E. MARCHAL, 1911; WETTSTEIN, 1924 b). As in *Funaria hygrometrica* (cf. p. 244) the Finnish form seems to be polyploid as compared with the Central European form. In the case of *A. serpens*, however, not merely tetraploidy but hypoploidy is present. The number  $n=22$  cannot be considered as a sporadic chromosome aberration because the same number has been established from material collected from several habitats. The possible morphological differences between the Finnish and Central European forms for the present have not been taken into consideration.

In the heterotypic metaphase of *Drepanocladus uncinnatus* there can be distinguished (Fig. 3 f) a heterochromatic »special» bivalent similar to those described above in the genus *Brachythecium*.

*Hypnaceae.* Eight species belonging to this extensive moss family have been investigated. The species and their chromosome numbers are as follows: *Isopterygium turfaceum* LINDB. (Fig. 3 h),  $n=11$ ; *Plagiothecium piliferum* (SW.) BR. & SCH. (Fig. 3 i),  $n=11$ ; *P. denticulatum* (HEDW.) BR. & SCH. (Fig. 3 j),  $n=10$ ; *P. denticulatum* var. *lactum* (BR. & SCH.) LINDB. (Fig. 3 k),  $n=11$ ; *Hypnum cupressiforme*



Fig. 3. — *a* *Brachythecium salebrosum*.  $n=13$ . — *b* *B. Starkei* ssp. *curtum*.  $n=20$ . — *c* *B. velutinum*.  $n=11$ . — *d* *B. populeum*, mesophilous ecotype.  $n=10$ . Observe one small bivalent and the symmetrical »special» bivalent. — *e* *B. populeum*, xerophilous ecotype.  $n=9$ . Here the ring-shaped »special» bivalent is asymmetrical and large. — *f* *Drepanocladus uncinnatus*.  $n=12$ . Observe the large ring-shaped »special» bivalent. — *g* *Amblystegium serpens*.  $n=22$ . — *h* *Isopterygium turfaceum*.  $n=11$ . — *i* *Plagiothecium piliferum*.  $n=11$ . A ring-shaped »special» bivalent can be seen. — *j* *P. denticulatum*.  $n=10$ . Observe the »special» bivalent. — *k* *P. denticulatum* var. *laetum*.  $n=11$ . Observe the openly ring-shaped »special» bivalent. — *l* *Hypnum cupressiforme*.  $n=10$ . — *m* *Ptilium crista castrensis*.  $n=11$ . The rightmost bivalent is the »special» bivalent. — *n* *Hylocomium splendens*.  $n=10$ . The leftmost bivalent is the »special» bivalent. In addition one asymmetrical bivalent can be distinguished.

— All the preparations made using the aceto-orcein squash method.  $\times 2300$ .

HEDW. (Fig. 3 l),  $n=10$ ; *Ptilium crista castrensis* (HEDW.) DNOT. (Fig. 3 m),  $n=11$ ; *Hylocomium Schreberi* (BRID.) MITT.,  $n=5$ ,  $2n=10$ , and *H. splendens* (HEDW.) BR. & SCH. (Fig. 3 n),  $n=10$ .

The family is cytologically almost unknown. KURITA (1937) has reported the number  $n=10$  for *Ptilium crista castrensis* from Japanese material. The number thus differs from the Finnish chromosome number. The other species belonging to this family whose chromosome numbers are known are *Hypnum imponens*,  $n=6-7$  (HEITZ, 1928) and *Hylocomium squarrosum*,  $n=6-8$  (HEITZ, l.c.).

The chromosome number  $n=10$  seems to be characteristic of the family. Aneuploid deviations from the chromosome number given can, however, occur. The halved chromosome number,  $n=5$ , in *Hylocomium Schreberi* cannot be understood as an indicator of a lower basic chromosome number. It represents an exceptional case where the number 10 has probably been reduced to 5 after fusion of the chromosomes. A detailed description of meiosis in this species will be published elsewhere.

The heterochromatic »special» bivalent discussed above (cf. p. 250) has been met with in several species belonging to the family, being, however, clearly lacking in the other species. It is to be found in all the *Plagothecium* species examined, in *Ptilium crista castrensis* and *Hylocomium splendens*. The shape of the »special» bivalent has been symmetrical in every case. As can be seen in Fig. 3 n there exists among the normal bivalents of *H. splendens* a strikingly asymmetrical one. As is known, the sex-chromosome system does not need to be asymmetrical, but where asymmetry has been met with we have reason to consider the XY-system of a dioecious species to be located in that chromosome pair. Here we have evidence that the »special» bivalent needs not, at least always, be connected with sex determination.

### Discussion.

The material presented on the previous pages does not widen our knowledge of the chromosomal relations of the mosses to any great extent. It does, however, throw light on the at present insufficiently studied question of the existence of intraspecific chromosome races among the mosses.

As LOWRY (1948) mentions, in the cases where corresponding diploid and tetraploid moss forms have been found, the bryological

taxonomists have distinguished two separate species. This is true especially in the genus *Mnium* where several such pairs of species have been met with (HEITZ, 1942; LOWRY, l.c.). The observations made in *Funaria hygrometrica* and *Amblystegium serpens* show, however, that polyploidy does not always lead to such phenotypical differences that, even according to the principles of bryological taxonomy, one would be warranted in making two separate species. It seems obvious that within the species mentioned intraspecific polyploid races occur in the northern part of their area.

*Brachythecium populeum*, again, represents the first case where numerical and structural differences have been observed between the genomes of the different ecotypes of a single moss species. JACHIMSKY (1935) has mentioned structural differences in the genomes of some races of the liverwort *Pellia epiphylla*. These races should, however, preferably be considered as geographical micro-races than as real ecotypes. There are clearly distinguishable differences in habit between the two *B. populeum* ecotypes examined. These differences, however, do not manifest themselves in the qualities important for the separation of different species. It may be thought, however, that the differences in question have been caused only by unlike environments in spite of the indisputable genotypical dissimilarity. The plasticity of the vegetative parts of the mosses is, it is true, frequently very wide. The real nature of the phenotypical differences between the ecotypes can be established only by performing culture experiments in similar environments.

The chromosome counts of the species *Drepanocladus uncinnatus* and *Hypnum cupressiforme* have been made from several ecotypes. No numerical differences between them have been observed, however. The possible structural differences between the genomes have not been subject to closer examination. It is possible that the differences, at least the numerical ones, between the genomes of the moss ecotypes are relatively rare.

Some of the chromosome numbers reported in this paper differ from the earlier counts. The discussion of the existence of possible chromosome races has been omitted in this connection because in such cases there may easily have been erroneous determinations of the chromosome number.

I wish to acknowledge my gratitude to the Director of the State Horticultural Institute, Professor O. MEURMAN, for the opportunity to



carry out this study at the Cytological Laboratory of the Institute. In addition, I wish to express my sincere appreciation to the Eemil Aaltonen Foundation for financial aid.

### Summary.

In the present investigation the chromosome numbers of 40 moss species, belonging to the Finnish bryoflora, have been established. They are given in the following list. In the list the chromosome numbers of the species marked with one asterisk have not been known earlier. The chromosome numbers of the species marked with two asterisks differ from those reported earlier.

	n	2n
<i>Polytrichum commune</i> .....	7	—
— <i>piliferum</i> .....	—	14
— <i>juniperinum</i> .....	—	14
<i>Bartramia pomiformis</i> var. <i>crispa</i> .....	8	—
*— <i>ityphylla</i> .....	12	—
** <i>Aulacomnium palustre</i> .....	12	—
<i>Mnium medium</i> .....	12	—
— <i>punctatum</i> .....	7	—
— <i>pseudopunctatum</i> .....	13	—
** <i>Funaria hygrometrica</i> .....	28	—
* <i>Pottia truncata</i> .....	25	—
* <i>Weisia controversa</i> .....	14	—
<i>Barbula unguiculata</i> .....	13	—
* <i>Paraleucobryum longifolium</i> .....	12	—
* <i>Dicranum spurium</i> .....	—	24
— <i>undulatum</i> .....	12	—
— <i>scoparium</i> .....	12	—
*— <i>majus</i> .....	12+5 a	—
* <i>Cynodontium strumiferum</i> .....	15	—
* <i>Amphidium lapponicum</i> .....	16	—
<i>Ceratodon purpureus</i> .....	13	26
* <i>Ulota curvifolia</i> .....	21+2 a	—
* <i>Orthotrichum speciosum</i> .....	6	—
* <i>Hedwigia ciliata</i> .....	22	—
* <i>Dichelyma falcatum</i> .....	10	—
* <i>Brachythecium albicans</i> .....	9	—
*— <i>salebrosum</i> .....	13	—
*— <i>Starkei</i> ssp. <i>curtum</i> .....	20	—
**— <i>velutinum</i> .....	11	—
*— <i>populeum</i> .....	10	—
*— » .....	9	—
* <i>Drepanocladus uncinnatus</i> .....	12	—

	n	2n
** <i>Amblystegium serpens</i> .....	22	—
* <i>Isopterygium turfaceum</i> .....	11	—
* <i>Plagiothecium piliferum</i> .....	11	—
*— <i>denticulatum</i> .....	10	—
*— var. <i>laetum</i> .....	11	—
* <i>Hypnum cupressiforme</i> .....	10	—
** <i>Ptilium crista castrensis</i> .....	11	—
* <i>Hylocomium Schreberi</i> .....	5	10
*— <i>splendens</i> .....	10	—

The Finnish form of the species *Funaria hygrometrica* studied is tetraploid and that of *Amblystegium serpens* hypotetraploid as compared with the corresponding Central European forms.

In *Brachythecium populeum* numerical and structural differences have been found between the genomes of two ecotypes.

In *Ulota curvifolia* two accessory chromosomes of very small type have been found.

In *Hedwigia ciliata* a chromosome pair has been encountered showing distance conjugation in meiosis.

In several pleurocarpic mosses there has been found a »special» bivalent in meiosis the origin of which is unique in the plant kingdom. It appears at prophase as a heteropycnotic ring-shaped bivalent on the surface of a nucleolus-like body which disappears later on. The anaphase separation of the »special» bivalent is normal.

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## The flax weeds and the origin of cultivated flax.

By HAKON HJELMQVIST.

The special flax weeds which occur in flax fields but are not or are only occasionally found in other habitats have been the object of several investigations (among others by ZINGER, 1909; THELLUNG, 1925; SINSKAJA and BEZTUZHEVA, 1931; ROTHMALER, 1944 and 1946). The question that has attracted special attention is that of the mode in which these weeds have arisen. In many cases it has been possible to establish without difficulty the presence of related parallel forms in other habitats, often as weeds in other crops, and the doubtlessly correct conclusion has then been drawn that the flax weeds have arisen by way of selection from these parallel forms (or a common ancestral form) under the special conditions of the flax fields. The fact that such peculiar weed forms have arisen just in the flax fields must be due to the very hard selection that has taken place here, owing to the special conditions prevailing in these fields as well as in a high degree to the great intervention of man in his attempt to remove all weeds both from the seed-grain and from the growing crop. Only those weeds have been able to survive which have shown a far-going conformity with the flax in their biology, in their habit (slender growth, loose inflorescence), in fruit- and seed-size, etc., and hence there has come into existence a group of weeds having very different relationships but all having a certain outward resemblance to each other and to the flax (*cf.* ROTHMALER, 1946). They are the result of a development that must have taken place in recent time; to some extent they are instances of what ROTHMALER calls »Artentstehung in historischer Zeit», and it is, then, quite natural that they have attracted great interest.

Another side of the matter, however, is also of great interest, *viz.* the phytogeographical question: From where do the flax weeds originate and what are their paths of migration? In this connection there also arises the problem of their relative age. These questions are of



importance for the still unsettled question of the origin of cultivated flax. With respect to the country of origin of flax widely different theories have been put forward up to most recent times: it has for instance been supposed to be Northern Eurasia (S. IVANOV, 1929), the Mediterranean region, especially its eastern part (ROTHMALER, 1944, 1946), Caucasia (HAYEK, 1908—1911), South-west Asia—Northern Africa (VAVILOV, 1926), Tibet (GUILLAUMIN, 1946). DE CANDOLLE made in 1883 the assumption of two areas of origin. (i) the Mediterranean region, (ii) the district between the Persian Gulf, the Black Sea and Caspian Sea, and in recent times CHEVALIER (1944) is apparently also inclined to assume that there are at least two different areas of origin.

The theories being so varying, it is of course desirable for the question of the origin of flax to be further elucidated by all available methods, and among others for this purpose an attempt will here be made to analyse — primarily from a phytogeographical point of view — the origin and earliest history of the flax weeds.

Of the genus *Camelina* two forms appear as flax weeds, *C. sativa* (L.) CR. s. str. (em. FR.) and *C. sativa* var. *foetida* (FR.) SCHMALH. (= *C. Alyssum* [MILL.] THELL.). The former is not such a pronounced flax weed as the latter; it is found in summer corn too and has besides been cultivated from ancient times. The relationships and mode of origin of these forms were already made the object of a searching investigation by ZINGER (1909). He points out that there is a series of related forms, from *C. microcarpa* ANDRZ., which also occurs in quite natural vegetation, over *C. sativa* var. *pilosa* DC. and *C. sativa* s. str., both of which on the one hand are cultivated and on the other occur as weeds, to the pronounced flax weed *C. sativa* var. *foetida*. As shown by ZINGER and other authors (latest, HIITONEN, 1947), these types also in their characters form links in a series from *C. microcarpa*, which is generally a winter annual, is very pubescent with both branched and unbranched hairs, has small, thick-walled fruits, small seeds and dehiscent capsules, to the summer annual, almost glabrous *L. sativa* var. *foetida*, in which the fruits are much larger, on long, out-standing stalks, thin-walled and incompletely dehiscent, and in which the seeds are much larger as well. *C. sativa* var. *pilosa* and *C. sativa* s. str. have an intermediary position. Var. *pilosa* is closer to *microcarpa* — it is cultivated as a winter crop —, *sativa* is closer to var. *foetida*. ZINGER holds a Lamarckistic view on the origin of this series; later investigators, of course, regard its development as the result of a selection of special genotypes. That var. *foetida*

has developed from *sativa* by way of selection in the flax fields is indubitable; the two forms are closely related and are connected by transitional forms, and var. *foetida* scarcely occurs outside the flax fields, or in cultivation either; attempts to cultivate this form have turned out badly (ZINGER, 1909, p. 37). With regard to *C. sativa* the mode of origin is not quite as clear, as it also occurs in other crops and is an old culture-plant, already known as such from prehistoric time (*cf.* STAUB, 1882; PAX-HOFFMAN, 1915), and easily escapes from cultivation. In certain cases it appears as though it had passed from weed into cultivated plant; in other cases, however, the culture-plant has probably been primary and the weed secondary. At all events it cannot be held as certain that *C. sativa* has always arisen as a weed in flax fields, and hence in the discussion of the flax weeds we had better leave this form out of account and only take var. *foetida* into consideration, which with certainty has arisen in this way. In its distribution, however, it must be compared with *C. sativa*, the form from which it has originated.

Both these *Camelina* forms are distributed over the greater part of Central, Northern and Western Europe (*cf.* ZINGER, 1909), but while var. *foetida* scarcely occurs outside Europe, *C. sativa* s. str. is spread right across Siberia (BUSCH, 1919) and is further found in the western part of Central Asia (BALABAJEV, 1925), in Caucasus and Transcaucasia (KUZNECOV, BUSCH, FOMIN, 1904—1910), in Asia minor (Armenia and Cilicia, TCHIHATCHEFF, 1860), as well as in Syria (THIÉBAUT, 1936). Also in south-eastern Europe *C. sativa* has a wider distribution than var. *foetida*.

In the Balkan Peninsula, thus, according to HAYEK (1927) the former occurs in Macedonia, Bulgaria (here according to URUMOV, 1928, in many localities), Dobrogea, Serbia, and Bosnia-Herzegovina, the latter only in the two last-mentioned districts and at least in Serbia according to PANČIĆ (1874) only at one locality. In Italy *C. sativa* is reported by FIORI (1923—1925) from the peninsula as well as from Sicily and Sardinia, though as more common towards the north, but var. *foetida* is only known from two districts in the northern part, the Bergamo-district and the neighbourhood of Parma.

Thus it is obvious that *C. sativa* has a considerably larger distribution towards the east and the south than var. *foetida*, which in comparison with the former has a more northern and western distribution. The relation between the two forms is especially thoroughly investigated so far as Russia is concerned (ZINGER, 1909; MALZEV, 1910; SINSKAJA and BEZTUZHEVA, 1931). According to SINSKAJA and BEZTUZHEVA, there is in Russia an obvious zonation between different

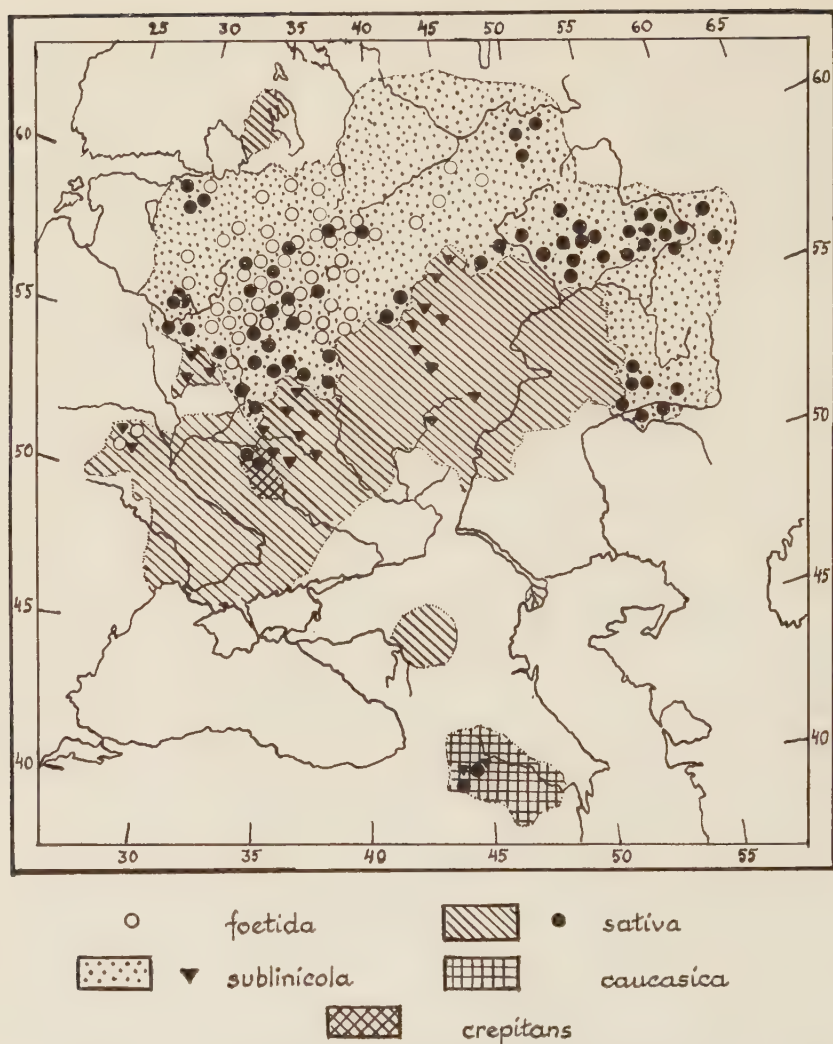


Fig. 1. Distribution in Russia of the *Camelina* forms admixed to flax. (According to SINSKAJA and BEZTUZHEVA, 1931.)

*Camelina* forms admixed to flax (see map Fig. 1). In the more southern part *C. sativa* s. str. predominates (together with two special varieties of this, var. *crepitans* and var. *caucasica*, with a smaller distribution). In the more northern part a form predominates that is intermediary between *C. sativa* and var. *foetida*, by ZINGER called *sublinicola*; the transition to *sublinicola* is put by the authors in connection with the

boundary between oil-flax (in the south) and flax for fibre (in the north), since it coincides to a certain degree with this. The quite typical var. *foetida* does not, however, occur in the whole of this northern region, but only in its north-western part (see the map), where it is found in rather scattered localities. To some extent, moreover, it is also found in the most western part of the *sativa* region.

These facts must be held to prove that in Eastern Europe var. *foetida* has arisen in its north-western part by way of selection from the related, partly very closely related, forms *C. sativa* and *sublinicola* and — as the older forms are found in the south-east, the youngest one in the north-west — that this differentiation has taken place during a migration from south-east to north-west. For the adjacent parts of Central Europe no such thorough investigations have been made as for Eastern Europe, and a very large material would be required for a full comparison. The available records, however, as mentioned, indicate a wider distribution towards the south-east of *C. sativa* than of var. *foetida* and for this reason the conditions are here probably parallel. At all events, *C. sativa* var. *foetida* has developed in European territory, the most south-eastern part, where it does not occur, falling out of account, and the conditions in Eastern Europe as well as in certain other regions, the Balkan Peninsula, *etc.*, argue in favour of the opinion that the differentiation has taken place by way of selection during a gradual migration from south-east to north-west.

As is shown by the numerous transitional forms, *C. sativa* var. *foetida* is weakly distinguished from *C. sativa* s. str., its ancestral form. This is confirmed by the genetical investigation that was carried out by TEDIN (1925). From this work it is apparent that completely fertile hybrids are obtained at crosses of var. *foetida* with *sativa* and also with a form ( $C_2$ ) that owing to its seed size and other characters seems to belong to var. *pilosa*. Only against *C. microcarpa* was a barrier of sterility established. It is accordingly obvious that *C. sativa* var. *foetida* — as probably also var. *pilosa* — has scarcely more than varietal rank and is a form that has arisen in comparatively recent times in the genus. A comparison between forms of different genera is of course very difficult, as the conditions may be different from genus to genus, but probably also at such a comparison the form is relatively young.

A parallel to *Camelina sativa* var. *foetida* is constituted — with regard to systematical position as well as to distributional conditions — by another flax weed, *Spergula arvensis* L. var. *maxima* (WEIHE)



MERT. & KOCH and by the related form *Sp. arvensis* var. *praevisa* (ZING.). As was elucidated in greater detail by ZINGER (1909), who also in this case has investigated the Eastern European conditions, there is within the genus *Spergula* a series of forms which proceeds from unspecialized weed forms over cultivated forms to flax weeds. To the original weed forms belong the usual form of *Sp. arvensis* var. *vulgaris* and the spontaneous *Sp. arvensis* var. *sativa*; these are characterized by a low habit, usually densely glandular-hairy stems and leaves, small seeds, completely dehiscent capsules. The culture-forms consist of the cultivated forms of var. *sativa* and var. *vulgaris*. They are of a somewhat higher habit, have a weaker hairiness, somewhat larger seeds, and capsules that open incompletely. The flax weeds var. *maxima* and var. *praevisa* are distinguished by little branching and many-articulated stems, up to 1 m high, glabrous as well as the leaves, large seeds, and large badly dehiscent capsules. The varieties *vulgaris* and *maxima* are denoted by papillae on the seeds in contradistinction to var. *sativa* and *praevisa*, in which such are absent; on this account it must be assumed that *maxima* has arisen from *vulgaris* and *praevisa* from *sativa*. Of course we should here, as in *Camelina*, regard the origin of the flax weeds as the result of a selection of certain suitable genotypes, though ZINGER at his time looked on the matter in a somewhat different way.

Also in their geographical distribution *Spergula arvensis* var. *maxima* and var. *praevisa* resemble *Camelina sativa* var. *foetida*.

Var. *maxima* occurs in Eastern Europe (KOMAROV, 1936) in the Ladoga-Ilmen district, in the upper Dnieper basin, in the upper Volga district, and in the Volga-Kama district; in addition it is found in western Siberia in the Irtysh district. According to ZINGER (1909), it is also known from Tomsk in Siberia and thus has a rather wide distribution from east to west. ZINGER (l.c.) states however that a comparative investigation has shown that only in the north-western districts (material from the Livonia, Pskov, Tver, Yaroslavl, Kostroma governments) is it quite typically developed, whereas farther to the south and the east (material from the governments Minsk, Orel, Kaluga, Tula, Vyatka, Tomsk) it has not so pronounced characteristics. Thus, we here have a complete parallel to the two *Camelina* forms *foetida* and *sublinicola*. Outside Russia var. *maxima* is spread throughout the whole of Central Europe and a great part of Northern and Northwestern Europe. The details of its distribution are not always clear, as var. *maxima* is not always kept distinct from other forms in the literature, but towards the south it reaches at least to Transsylvania (SCHUR, 1866), Herzegovina (BECK, 1909), and Portugal (ROTHMALER, 1944) and towards the north to England and in Scandinavia at least to Örkedalen in Norway, Ångermanland (Överlänns) in Sweden, and Karlsö (LUTHER, 1948) in Finland. Moreover, in recent times it has spread to other continents.

*Spergula arvensis* var. *praevisa* has a distribution that is very reminiscent of that of var. *maxima*. Yet it is somewhat more western.

In Russia ZINGER (1909) knows the form only from the governments Yaroslavl, Tver, Pskov, and Smolensk; in recent time it has according to KOMAROV (1936) been brought with linseed eastwards so far as to Perm. According to KOLOKOLNIKOV (1931), it does not at all occur in the Vyatka district (rather far in the east), whereas var. *maxima* is common there. The distribution outside Russia is incompletely known, owing to lack of data, but the form is recorded from western Galicia (ZAPALOWITZ, 1911, as *Sp. arvensis* var. *maxima* f. *laevis*), from France (the Loire district, from where the first description was made, see ZINGER, 1909), and from northern Portugal (ROTHMALER and P. SILVA, 1939; ROTHMALER, 1944). In Scandinavia it also occurs; specimens have been seen by the present writer from Sweden, Skåne: Barkåkra, Västergötland: Skånings-Åsaka and Gotland: Sproge. The seeds are here, however, not more than up to 1.5 mm broad, whereas in var. *maxima* they often exceed this measure.

The difference that is found in the distribution of var. *maxima* and var. *praevisa* and that is conspicuous in the border district in Eastern Europe, where var. *maxima* penetrates farther to the east and the south than var. *praevisa*, is possibly due to the different distribution of the two ancestral forms, var. *vulgaris* and var. *sativa*. As was already pointed out by NICHOLSON (1880) and later by other authors (see for instance SCHISCHKIN, 1936), var. *vulgaris* has a much wider distribution towards the east and the south, far outside the limits of Europe, than var. *sativa*, which is more northern and northwestern and is dominant or is present alone for instance in the northern part of Britain (NICHOLSON, 1880; MOSS, 1920); the same is the case in Sweden. Also in Russia the difference is perceptible according to ZINGER (1909), var. *vulgaris* being more predominant in the southern area of distribution, var. *sativa* apparently prevailing in an investigated district more to the north. This may possibly explain the more northern and western distribution limit of var. *praevisa* in this region.

For var. *maxima* as well as var. *praevisa*, however, it is true that they have a northwesterly orientated distribution compared with the ancestral forms. Like *Camelina sativa* var. *foetida*, var. *praevisa* as well as the typically developed var. *maxima* must have arisen in Europe, probably in the northwestern part of Eastern Europe. The fact that var. *maxima* is more typically developed in northwestern Russia than farther to the east and the south indicates that in this case, too, we are justified in considering that a differentiation has taken place during an advance towards the northwest.

Quite recently a new *Spergula* species, *Sp. Camarae*, occurring as

flax weed, has been described by ROTHMALER (1944) from northern Portugal. The present writer has not seen any material of this species, but it is said to resemble *Sp. arvensis* var. *maxima* and var. *praevisa*, which occur in the same district, but differs from these in having larger seeds (2.1 to 3.0 mm broad, as against 1.5 to 1.8 for var. *maxima*), which also are of a somewhat deviating shape, »subreniformia» and flattened, and somewhat broader-winged. As papillae are absent on the seeds, the species is closest to var. *praevisa*. Perhaps it should rather be regarded as having arisen from this by way of a further differentiation and perfection of the flax-weed characters. *Sp. arvensis* var. *praevisa* often has a somewhat larger wing at the seeds, too, than var. *maxima*, and from western France (where it was at first described by BOREAU under the name of *Sp. linicola*) some other features are reported: »seminibus orbiculato-subreniformibus», seeds up to 2 mm broad (ZINGER, 1909, p. 266, according to BOREAU and other sources), implying a similarity to *Sp. Camarae* and perhaps to be interpreted as a transition to this. The fact that the seeds of *Sp. Camarae* are not only larger, but also of a more flattened form than in var. *praevisa* has an analogy in another flax weed, *Sinapis alba* \* *dissecta* in comparison with *S. alba*, and can in both cases be thought to be the result of a selection of those qualities that are most agreeing with those of the flax.

The *Spergula* forms treated are united by transitional forms and weakly separated from each other. They have all been proposed as species of their own, but in later times especially the *vulgaris* and *sativa* forms are often considered so closely related that they are not given any systematic value whatever. Without doubt there is no essential difference between them, but, as they show a marked deviation in the qualities of their seeds and their geographical distribution is somewhat different, too, they should apparently be regarded as separate varieties. On the other hand, it has been proposed also by later investigators (ROTHMALER and P. SILVA, 1939; ROTHMALER, 1944; HYLANDER, 1945, yet with some reservation) that the *maxima* form should rank as a species of its own, divided by ROTHMALER and P. SILVA into two varieties, var. *maxima* and var. *praevisa*, whereas the latter is considered by HYLANDER (1945), as well as by ZAPALOWITZ (1911), only to be a form, f. *laevis*, of *Sp. maxima*. The characters by which *maxima* differs from *vulgaris* are however mainly of quantitative nature, and transitions are found between them, and of the *praevisa* form it must be presumed that it has not arisen from *maxima* but from *sativa*, in the same way as *maxima* from *vulgaris*; between *sativa* and *praevisa*,

too, transitions are to be found (*cf.* ZINGER, 1909, also seen from Sweden). In view of this and to avoid a contradiction between the systematics and the relationships, it seems best to regard all the four investigated forms as varieties of the collective species *Sp. arvensis* L. For the *praevisa* form a new combination is then obtained: *Sp. arvensis* L. var. *praevisa* (ZINGER) n. comb. [*Sp. linicola* BOREAU in Mém. Soc. Acad. Angers XX 1865, p. 14; *Sp. vernalis* var. *linicola* GÜRKE in RICHTER-GÜRKE Pl. Eur. II 1899, p. 200 (non *Sp. arvensis* var. *linicola* SCHWARZ in Abh. Nat. Ges. Nürnberg. X 5, 1897, p. 126); *Sp. praevisa* ZINGER in Act. Hort. Jurjev, VII 1906, p. 85; *Sp. arvensis* L. var. *maxima* WEIHE for. *laevis* ZAPŁOWICZ, 1911; *Sp. maxima* WEIHE var. *praevisa* (ZINGER) ROTHMALER & P. SILVA, 1939; *Sp. maxima* WHE. var. *laevis* (ZAP.) ROTHMALER, 1944; *Sp. maxima* WHE. f. *laevis* HYLANDER, 1945]. — At all events it is obvious that *Spergula arvensis* var. *maxima* and var. *praevisa* are forms that have arisen in comparatively recent times.

A certain correspondence to the above-mentioned flax weeds is formed by *Silene cretica*, occurring in the flax fields of the Mediterranean region. In this case, too, there is a series of different forms, which have sometimes been regarded as species. On the one hand there is the pronounced flax weed *S. annulata* THORE, which is sometimes regarded as a subspecies of *S. cretica* (HAYEK, 1908—1911; HEGI, 1910—1912), often as a variety (FIORI, 1923—25; HAYEK, 1927), and in some cases, owing to the transitional forms observed, is completely united with *S. cretica* (ROHRBACH, 1868; BRIQUET, 1913). It is a decided annual, often strongly and somewhat irregularly ramified in the upper part, the fruit is short and broad, almost globose, reminiscent of a flax fruit, with a very short carpophore (about  $\frac{1}{5}$  to  $\frac{1}{7}$  of the capsule), the seeds are large, nearly two mm long, with a slight dorsal furrow between the salient edges and with round, low warts (Fig. 3 e, f), and the petals are deeply cleft (*cf.* LINDMAN, 1891, whose statements on *S. cretica* refer to this form, judging from material in Herb. Stockholm). According to the opinion of the present writer, it should be regarded as a subspecies, *S. cretica* ssp. *annulata* (THORE) HAYEK, on account of the marked differences especially in the seed structure and the partly different distribution area.

The main form, *S. cretica* s. str., by FIORI (1923—25) named var. *typica*, is distinguished by its fruit being ovate, longer and narrower than in subsp. *annulata*, with a carpophore of moderate length (the



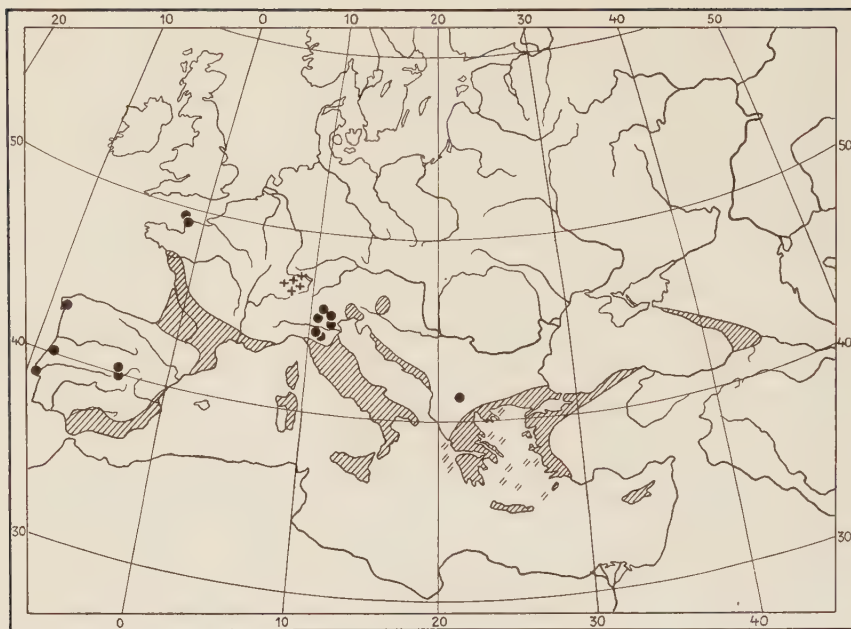


Fig. 2. Distribution of *Silene cretica*. The crosses denote the finds in the Swiss lake-dwellings.

capsule at least three times as long as the carpophore). Its petals are often slightly emarginate. The seeds are small, scarcely 1 mm long, more or less flat on the dorsal side, and with elevated warts (Fig. 3 *a, b*). It occurs both in natural vegetation and in flax fields.

A third form is *S. tenuiflora* GUSSONE, which by BOISSIER (1867) was held to be a species of its own, but by ROHRBACH (1868), in his monograph on the genus, was united with *S. cretica* and is regarded as a variety of the latter by some other authors (CESATI-PASSERINI-GIBELLI, 1867; FIORI, 1923—25; HAYEK, 1927; RECHINGER, 1943). It differs from *S. cretica* s. str. (BOISSIER, *l.c.*; ROHRBACH, *l.c.*; FIORI, *l.c.*; *etc.*) mainly by the capsule being smaller, more oblong-ovate, only about 2—4 times as long as the carpophore. From the main form there is however no sharp demarcation (*cf.* ROHRBACH, *l.c.*); it certainly should only be regarded as a variety. Yet it does not occur in arable land, at least as a rule (GUSSONE, 1826; POJERO, 1889), but in grassland, open land, *etc.*

Another form, which has not been broken out of *S. cretica* but is rather deviating, is a small-flowered form occurring in Crete (Lassithi,

Mount Katharos, coll. LEONIS 1900; near Youchtas, in rocks, coll. WALL 1930) and Cyprus (Pana Platraes, coll. WALL 1930, Herb. Stockholm) with a quite different habit, low, richly branched from the base, with few-flowered stems, certainly biennial. The fruit is ovate, about four times as long as the carpophore. The petals are rather deeply cleft. It appears to be an original form of var. *typica*, occurring in natural vegetation.

The distribution of *Silene cretica* is shown in Fig. 2, constructed on the basis of general handbooks and herbarium specimens. Owing to the changes of distribution caused by cultural conditions the map must be approximative only, as is also the case with the other maps of the flax weeds. The distribution area is for the greater part situated within the Mediterranean region. Outside this region, however, *Silene cretica* is also encountered in the southern part of Styria (HAYEK, 1908—1911), in southern Tyrol (DALLA TORRE-SARNTHEIM, 1909) and in southern and western France, where many occurrences are known.

The different forms, however, are not evenly distributed in this area, but show a certain geographical difference. Subsp. *annulata*, thus, dominates in the north: In France all specimens seen by the author, as far as they were determinable, have been more or less typical *annulata*, and THELLUNG (1912) states that first and foremost this form occurs in France. In Styria (HAYEK, 1908—1911) and Tyrol (DALLA TORRE-SARNTHEIM, 1908) only subsp. *annulata* is found. The subspecies is however spread in more southern districts, too: in Italy it occurs down to Sicily in the south (for instance Tortorici, spec. by TODARO no. 588), and in the Balkan Peninsula it also occurs (HAYEK, 1927), though the main form prevails here; even from Crete a collection is at hand that in any case is very close to ssp. *annulata* (La Canée; REVERCHON no. 1518). *S. cretica* s. str. occurs in the whole distribution area except the most northern part, and together with it var. *tenuiflora* is found in southern Italy and in Greece (ROHRBACH, l.c.; according to LINDMAN, l.c., it occurs in Spain, too, but this author takes it in a wider sense), and the previously mentioned biennial form at Crete and Cyprus. With regard to the original forms that occur in the eastern Mediterranean region and the mosaic-like mixture of flax-weed forms and wild forms extending even here we must suppose that the flax weeds have their first origin in this district and have been more and more differentiated out during an advance towards the west and north. The development must presumably have proceeded from the wild forms of *S. cretica* s. str. over its weed forms to the definite flax weed subsp.



Fig. 3. *a-f* *Silene cretica*, seeds, *a-b* of wild-form from Rhodes, *c-d* from the lake-dwellings at Robenhausen, *e-f* of *ssp. annulata*; *g, i, k, m, n*: *Silene linicola*, flower, part of calyx, part of the stem surface, seed; *h, j, l, o, p*: *S. crassipes*, the same; *q-r* seed of *Silene gallica* var. *linophila*, *s-t* of *S. gallica*. *g, h*  $\times 2$ , *i, j*  $\times 5$ , the others  $\times 15$ .

*annulata*, which in fruit and seed size as well as in habit approaches closely to flax.

According to HEER (1865, 1872), seeds of *Silene cretica* have been met with in the Swiss lake-dwellings Robenhausen (from the Stone and Bronze Age) and Niederweil (neolithic), partly in great abundance and mixed up in flax bundles. If these statements are correct, we should here have a means of estimating the absolute age of the weed. The correctness of the diagnosis is however disputed by NEUWEILER (1905, also 1924), who however does not furnish any other; he points out that

the *Silene* seeds from the lake-dwellings, reported by him also from Steckborn, Baldeggersee, Burgäsch, Baden, are of a deviating shape and size: they have a convex dorsal side, whereas in *S. cretica* this is concave with two edges: they have, further, more acute warts than this species and a more regular shape, and they are also smaller (length up to 1.4 mm as against an average of 1.73 mm for *cretica*). This difference between the *Silene* of the lake-dwellings and *S. cretica* is doubtless present, if by *S. cretica* is meant the form that is common as flax weed, subsp. *annulata*. But the *Silene* seeds from the lake-dwellings show, as I have had an opportunity to observe at an investigation of material from Robenhausen<sup>1</sup>, great agreements with other *S. cretica* forms. As is shown by Fig. 3 *c—d*, the seeds agree in their shape and surface sculpture almost completely with seeds of *S. cretica*, a form from a cypress forest at Rhodes (Fig. 3 *a, b*), the seeds of this form are only of a still smaller size. In both cases the dorsal side is more or less flat, the shape is regular and the warts are acute. The lake-dwelling seeds may apparently be well fitted into the range of *S. cretica*, if the species is taken in a wide sense; HEER's determination was certainly correct. In their morphology the seeds are intermediate between the original wild form and the most derived weed form, ssp. *annulata* (Fig. 3 *e, f*), though they are closer to the former. By way of selection the flax weed, of course, has developed further after the time of the lake-dwellings, a development that has proceeded towards larger seeds with more even surface but with more irregular outline; the irregular structure has possibly implied a greater »coefficient of voilure», according to the Russian investigators an especially important quality, and on this account also had a selection value.

It is a fact of great interest that in neolithic times *S. cretica* occurred in a district (in Switzerland) where it is not at all found nowadays. HEER (1872) explains this by the supposition that there has been a repeated import of linseeds from the Mediterranean region and that the *Silene* seeds have then accompanied them. The fact may also be explained by the more favourable climatic conditions in the later Stone Age (*cf.* BERTSCH, 1947, p. 201).

As at the time of the Swiss lake dwellings *Silene cretica* was already transformed into a somewhat derived weed form, with larger seeds than the wild-form, its absolute age must be considered high. It is without doubt one of the oldest flax weeds.

<sup>1</sup> Kindly put at my disposition by Prof. WALO KOCH, Zürich.



*Silene linicola* belongs to those flax weeds which have a very restricted distribution area. The species occurs (map Fig. 4) in southern Germany in Bavaria (cf. VOLLMANN, 1914), Wurtemberg (MARTENS-KEMMLER, 1865), and Baden (DÖLL, 1862), further in Luxemburg (NYMAN, 1889), in some Austrian countries, viz. Carinthia (PACHER and JABORNEGG, 1887), Styria (HAYEK, 1908—1911) and Tyrol (DALLA TORRE and SARNTHEIM, 1909), and occasionally in Upper and Lower Austria (KOCH, 1892; BECK, 1890), and in northern Italy at a few localities (PARLATORE, 1890—93, and herbarium material). In Switzerland it is lacking, and in Germany and Austria it is everywhere rare (cf. HEGI, 1910—1912); at some old localities in Bavaria it has in later times disappeared (VOLLMANN, 1914).

As also is the case with *Cuscuta epilinum*, it has not either for *Silene linicola* been possible to establish any parallel form in other vegetation, from which the weed plant adapted to the flax fields can have originated. In ROHRBACH's monograph of the genus *Silene* (1868), an old but valuable work, *S. linicola* is referred to the series *Leiocalycinae* of the section *Dichasiosilene*; *S. linicola* cannot, however, derive its origin from any other of the species referred to this by way of selection in the flax fields. The other species deviate *inter alia* in the stem being generally glabrous, whereas stem and leaves of *S. linicola* are shortly pubescent; thus there exists quite a contrary condition to that generally found between wild-form and flax weed: the weed has as a rule reduced pubescence. Possibly one species, *S. Almolae* from Spain, could be reminiscent of *S. linicola* as to pubescence and some other qualities; it shows however considerable deviations, too, for instance in the seed structure (WILLKOMM, 1852—1854). Thus, there is apparently no close affinity between this species and *S. linicola*, and nor is this seemingly the case with the later-described species that are referred to the series.

On the other hand there are great similarities between *S. linicola* and a species that was referred by ROHRBACH (*l.c.*) to the related series *Lasiocalycinae*, viz. *S. crassipes* FENZL, growing in Syria and Palestine. C. A. M. LINDMAN (1891) was the first to draw attention to the agreement between these two species, which were observed by him in cultivation side by side. In his opinion many of the differences between them are merely relative. The most important divergences are, according to him (*l.c.*, p. 8—9), that the pedicels are considerably longer in *S. linicola*, the dichasium thinner, the veins of the calyx less prominent (the difference in this respect is however inconsiderable in the opinion of

the present writer) and less pubescent than in *crassipes*, the calyx in fruit stage with a broader, truncate base and in the upper part as well as the enclosed fruit broader and rounder. LINDMAN regards the two as separate species, though closely related to each other.

A more searching comparison of some details of the two species affirms the view of LINDMAN that they are closely related. In many cases there exists a striking agreement. The flower type, thus, is the same (Fig. 3 *g, h*), the calyx lobes are somewhat different but on the whole of similar appearance, round-obtuse and scarious-marginate and with the same pubescence (Fig. 3 *i, j*), the petals are of similar shape, the stem has the same characteristic hairs (Fig. 3 *k, l*), short and downwards-bent (though more weakly developed in *linicola* as well as the pubescence of the leaves), the seeds are of the same structure (Fig. 3 *m—p*). As to the different density of the inflorescence there is, moreover, some variation in *S. crassipes*: in a collection from Orfa, Nimrud Dagħ (SINTENIS no. 823) the pedicels above the bracteoles are as usual short (up to about 2 mm), but the internodes beneath the bracteoles are somewhat extended (up to 2.5 cm), the inflorescence thus being less dense than in other cases. There is no doubt that the two species stand very near to each other.

It is however possible to go a step farther than only to the establishing of the close affinity. A scrutiny of the deviations from *Silene crassipes* which are found in *S. linicola* reveals that for the most part they just consist of such as generally distinguish the flax weeds from their parallel forms in other vegetation. The slender habit, the long pedicels, the thin inflorescence have their correspondence in other flax weeds (and have their biological advantage therein that the inflorescence thus spreads out at the level of the flax flowers and does not differ very much from that of the flax). The more rounded capsules, more like flax capsules, the larger seeds, and the weaker pubescence are features that also as a rule characterize the flax weeds as well as the somewhat narrower leaf-form which generally distinguishes *S. linicola* from *S. crassipes*. All these characters, thus, may have arisen by way of selection from *S. crassipes* in the flax fields, and the few other divergent features that are found may be due to the fact that the selection by chance has taken its origin from a *S. crassipes*-type with such characteristics.

Thus we arrive at the result that *S. linicola* has developed from *S. crassipes* through a selection — of long duration — in the flax fields, it then of course being possible that the form of *S. crassipes* which has



Fig. 4. Distribution of *Silene linicola* (circles) and of *S. crassipes* (crosses). Open circles accidental occurrences. The locality for *S. crassipes* in Thrace is indicated approximately.

not been transformed into a flax weed has also undergone certain changes in the course of time.

While there are thus strong morphological reasons to assume a descentance of *S. linicola* from *S. crassipes*, it appears as if the phytogeographical conditions raise difficulties in the way of such a theory. The distribution areas of the two species are widely separated from each other: the one has a limited extension in the central parts of Europe, the other has its centre in Syria and Palestine. If *S. linicola* has arisen from *S. crassipes* by way of selection in a migration from the one district to the other, there should be some remaining occurrences in the vast intervening area. One or two such also exist. Thus, according to HAYEK (1927), *S. crassipes* occurs in Thrace, in cultivated fields (the primary record has not been found by the writer, is perhaps not published). It is of course then also very probable that there are solitary localities in Asia Minor too, between Thrace and Syria, a region that floristically is not very well explored. On the other hand, there is a

record of a locality for *S. linicola* that is far to the east. SCHUR (1866) states that it occurs in flax fields in the so-called Szekler-land in Transylvania, where it has been collected near the village Remete. A later author (SIMONKAI, 1886), however, reports the species as not spontaneous in Transsylvania; he is evidently of the opinion that its occurrence there is the result of an occasional import. Yet it is also possible that it may be a remnant of an old occurrence; as a matter of fact this appears more probable in view of the remote situation of the country and of the fact that it was an old flax-growing district, where other flax weeds, e.g. *Lolium remotum* and *Camelina*, were common at that time (SCHUR, l.c.). There seems to be no obstacle to the supposition that *S. cretica* has arisen by way of selection from a *S. crassipes* population during an immigration as flax weed over Asia Minor, the northern Balkan Peninsula and the Danubian countries. It must be presumed that the development has been about the same as may still be observed in the case of *S. cretica*: with a removal from the original native country a transformation takes place which, although by no means proceeding regularly, on the whole brings about an approach to the more derived flax-weed form. Consequently this is most pronounced in the regions most distant from the country of origin, as far as *S. linicola* is concerned those districts where the species is still occurring. That it has been able to survive here, whereas it has disappeared over other large areas, is, thus, partly due to its more perfect adaptation to the special conditions that has been reached here. This is certainly also due in part to the fact that the districts in southern Germany and the Alps where *S. linicola* has retained its position are districts with old-fashioned agriculture: for instance several old culture-plants, *Triticum Spelta*, *Tr. monococcum* and *dicoccum*, and the winter flax, *Linum usitatissimum* ssp. *bienne*, have still been under cultivation in these districts in late times.

Besides the above-mentioned, one more flax weed has developed in the genus *Silene*, viz. *S. linophila* ROTHM. The species was described by ROTHMALER (1944) from Portugal, where it occurs in winter flax belonging to *Linum humile*; according to this author it is probably also to be found in Spain and, introduced, in Argentina. It is closely related to *S. gallica* and differs from it in the inflorescence being more few-flowered, the seeds (Fig. 3 *q-r*) twice as large,  $1\frac{1}{2}$  mm long or more, and in the absence of the long hairs which generally occur in *S. gallica* (especially at the calyx) intermingled with short ones; in



*linophila* there is only a short (to a great extent glandular) pubescence. These characters do not apparently imply any great deviation from *S. gallica*. This species is very polymorphous. JORDAN and FOURREAU (1866, cf. 1866—68) described fourteen microspecies, which were regarded by ROUY and FOUCAUD (1896) as varieties, and two of these are said to have only glandular hairs at the calyx. *S. linophila* seems to be comparable with these, though also distinct by its seed-size, and should perhaps rather be given varietal rank. Its relation to *S. gallica* is reminiscent of the condition between *S. cretica* of the lake-dwellings and the wild-form of this species; as in this case the seeds are considerably larger in the flax weed, but otherwise of the same structure. It has without doubt developed by way of selection in the flax fields, but apparently it is a form that has arisen in recent times and with locally restricted distribution.

*Sinapis alba* ssp. *dissecta* (LAG.) BONN. is a flax weed occurring in the Mediterranean region, eastern Europe and Causasia. It is closely allied to *Sinapis alba* but its relation to this species is somewhat disputed. It was described as a species of its own by LAGASCA (1816, as *Sinapis dissecta*) and likewise by TURCZANINOW (1854, as *Sinapis ucranica* CZERN.) and is regarded as such by many authors, among others PARLATORE (1890—93), who emphasizes that it is a distinct species and not a variety of *S. alba*, and by SCHULZ (1919), in his monographic treatment of *Cruciferae-Brassicaceae*. On the other hand, COSSON (1883—87) is doubtful about its specific value and BRIQUET (1913) regards it as a subspecies of *S. alba*, with regard *inter alia* to the fact that at Corsica there is found a transition between the *alba* and *dissecta* types, by him called *S. alba* var. *corsica*. Still longer in the same direction goes SINSKAJA (1928), who is of the opinion that *Sinapis dissecta* cannot be maintained even as a subspecies or variety but must be entirely conjoined with *S. alba*. In support of this the crosses are mentioned (cf. also in KOMAROV, 1939) which have been produced by the author; they were quite fertile and in the second generation a free combination was observed of the separating characters, which apparently were dependent on a small number of genes.

The characteristics in which ssp. *dissecta* differs from *S. alba* are in the main the following: Plant more slender, less pubescent (glabrescent), leaves deeper and narrower incised, pinnati-partite with lanceolate to oblong-lanceolate segments, these often more incised than in *S. alba* and the terminal lobe scarcely larger than the lateral ones as

in *S. alba*. Fruit-stalks longer and thinner, upwards-curved (not straight outstanding). Pods (Fig. 6 c—f) glabrous or sparsely pilose (in *alba* [Fig. 6 a—b] densely hirsute with more vigorous hairs), more broadly rounded, generally without seeds in the beak. Seeds larger than in *alba*, somewhat flattened, reddish-brown, not yellow. In addition it is stated from the Russian district that the petals are narrower than in *alba* (SINSKAJA, 1928) and the pods incompletely dehiscent (MALZEV, 1924). Anatomical differences of the seeds are described and figured by GRAM (1894, *cf.* also VUILLEMIN, 1904): in *ssp. dissecta* the cells and wall-thickenings of the mechanical tissue are of different height, which makes the testa slightly reticulate whereas they are of equal height in *alba*; these cells as well as the underlying tissue also contain a reddish-brown pigment in *ssp. dissecta*.

The great majority of these deviating characters of the *dissecta* form may be explained as having arisen through selection within the original *alba*-type under the special conditions of the flax fields. The slight pubescence, the narrow-lobed leaves, the slender growth, the large and somewhat flattened seeds, all are characters that have their analogy in the deviations shown by other flax weeds from their ancestral forms and have no doubt, like these, arisen by way of selection. The colour of the seeds may also be explained by selection into similarity with flax. According to MALZEV (1924), the form shows a far-going agreement with flax in its biology, too. With regard to the transitional forms that are found in different districts and the fertile crosses produced by SINSKAJA, it is apparently not correct to give the *dissecta* type a full specific rank. On the other hand, it is in several respects markedly different from the typical *S. alba* and also shows a somewhat deviating anatomical structure of the seeds. This seems to be sufficient reason to regard it, in accordance with BONNIER (1911), BRIQUET (1913) and HEGI (1913—1919), as a subspecies.

*Sinapis alba* has a considerably wider geographical distribution than *\*dissecta*. The fact that it has for long been cultivated has of course contributed to its dispersal.

It occurs (HEGI, 1913—1919; SCHULZ, 1919) in Southern Europe, West Asia to East India, and, cultivated and naturalized, also in Central and Northern Europe and several extra-European districts. Usually it grows as a weed, sometimes also in flax fields. From Palestine and some other districts it is stated, however, (BORN-MÜLLER, 1924) that it may appear in quite natural vegetation, ravines, *etc.* According to SINSKAJA (1928) in Palestine and Transjordan there is found a deviating form that should be referred to a special variety, *var. orientalis* SINSK. It is very probable that we here have the native country for *S. alba*.

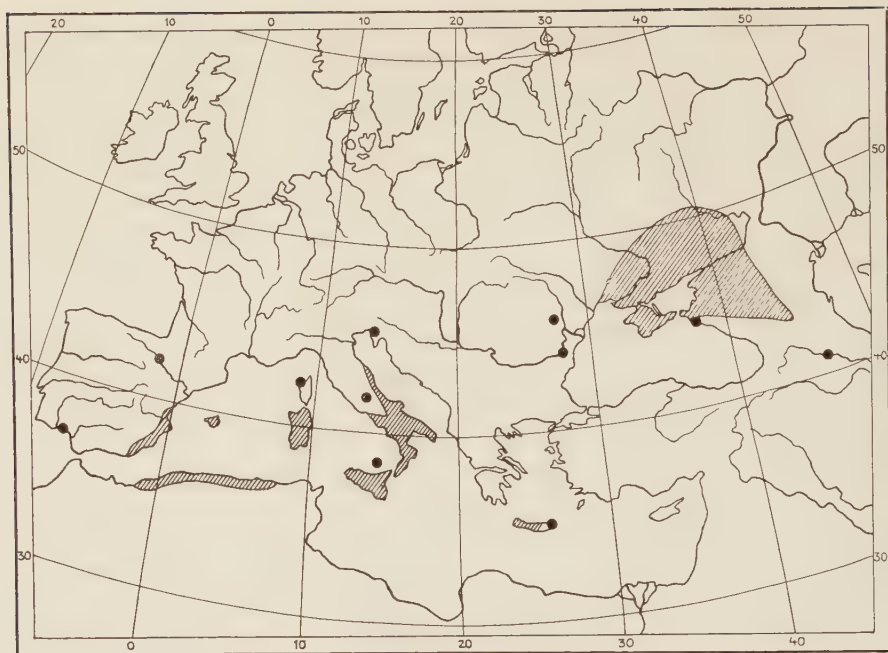


Fig. 5. Distribution of *Sinapis alba* subsp. *dissecta*.

The distribution area of ssp. *dissecta* (Fig. 5) is divided into two regions, a Mediterranean and an East-European one. In the Mediterranean region it occurs in the western part, and further at Crete, especially the western part of the island (RECHINGER, 1943). In addition there are both in the Mediterranean region and in more northern districts many occasional occurrences. In its East-European range subsp. *dissecta* occurs mainly in southern Russia, where it is recorded from 7 governments, and further in Ciscaucasia and sporadically in Transcaucasia. Somewhat remote from the Russian distribution area are two occurrences in Rumania, viz. in Lower Moldavia (KANITZ, 1879—81, according to GUÉBHARD) and in Dobrogea at Rassova, where it is found in flax fields (KANITZ, 1879—81, and Herb. spec. of Brothers SENTENIS 1875).

In the literature it is stated that *Sinapis alba* \**dissecta* is cultivated in southern Russia (VUILLEMIN, 1904; HEGI 1913—1919, p. 206). According to SINSKAJA (1928), it is however not known in cultivation, though it occurs that the weed-plant is gathered in and used. MALZEV (1924) reports that in some districts of southern Russia it is such a

common flax weed and, owing to the difficulty of removing the seeds at winnowing, is sown to such a large extent year after year that the farmers can be said to cultivate it »against their will». These conditions have probably given rise to the statement of its cultivation.

That *Sinapis alba* \**dissecta* occurs in two separate distribution areas is probably due to the fact that it has arisen on one hand in Eastern Europe (South Russia), on the other in the Mediterranean region (the western part), and not to an introduction by human agency from the one region to the other. Thus, there are in both areas transitions between the *alba* and *dissecta* types, and in both there is a parallel variation between a form with hairy pods, f. *Lagascana* (ALEF.) THELL., and a form with glabrescent pods, f. *subglabra* (BRIQ.) THELL. in HEGI. It is also quite natural that, in the case of a wide-spread species like *Sinapis alba* being subjected to selection under similar conditions (in flax fields) at many places, the form developed through selection will arise in more than one district. The occurrence at Crete is probably secondary, of western origin, as in the main the distribution here is restricted to the western part and has not at all spread to surrounding districts.

As regards, finally, the age of ssp. *dissecta*, it is obvious, owing to there being no sharp line of demarcation as against *S. alba*, that it does not belong to the oldest flax weeds, as for instance *Cuscuta epilinum* and *Lolium remotum*, which are good and independent species. On the other hand, it is apparently more divergent from *S. alba* than for instance *Camelina sativa* var. *foetida*, belonging to the same family, is from *C. sativa*. It seems to be rather, even if not very, old in comparison with other flax weeds.

Another flax weed of the genus *Sinapis* is found in the Mediterranean region, viz. *S. Allionii* JACQ. This species occurs in Egypt, where it is spread in the Nile Delta, Fayûm, and the narrower alluvial Nile-Valley (BOISSIER, 1867; MUSCHLER, 1912). It is closely related to *S. arvensis*, *Sinapis turgida* DEL.=*S. Allionii* var. *turgida* (DEL.) BOISS. in some respects forming a transition, and is often regarded as a variety of *arvensis*. It differs from *arvensis* in the fruits being short and rounded (Fig. 6 g), the leaves deeply pinnatipartite and the whole plant glabrous. The seeds are also in general larger (SCHULZ, 1919). These are thus characters that distinguish many flax weeds and they have quite certainly arisen through selection of forms suitable for the flax fields. The difference between *S. Allionii* and *S. arvensis* in fruit and leaf



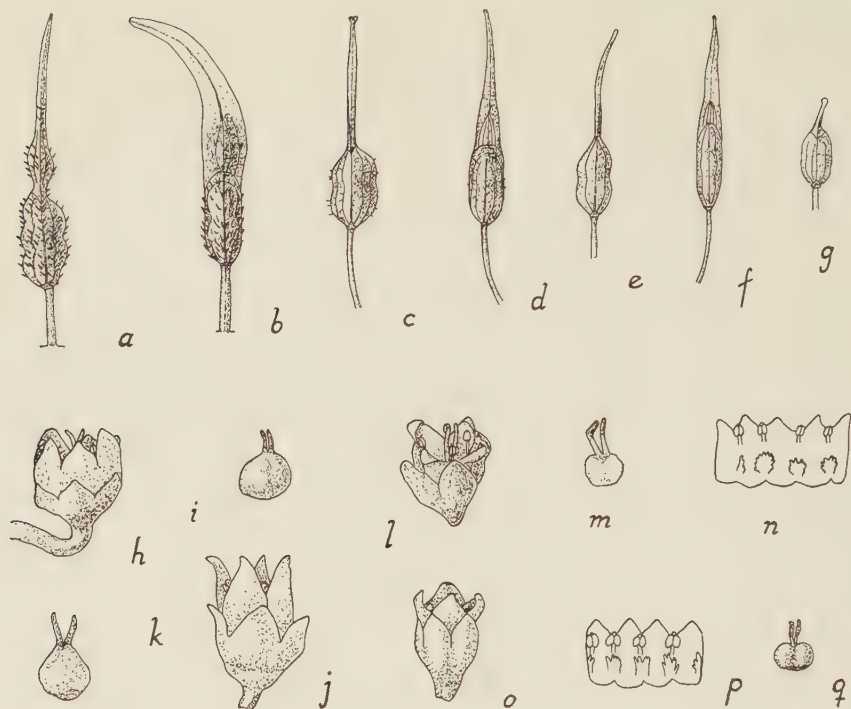


Fig. 6. *a—b Sinapis alba*, fruit from two sides; *c—d* the same of *S. alba* ssp. *dissecta* from Sicily; *e—f* pods of the same from Rumania, Rassova; *g* fruit of *S. Allionii*; *h—i Cuscuta pedicellata*, flower and pistil; *j—k C. Kotschyana* var. *caudata*, the same; *l—n C. palaestina*, flower, pistil and corolla unrolled; *o—q C. kurdica*, the same. *a—g* nat. size, *h—q*  $\times 5$ .

shape is rather great, greater than between *S. alba* and ssp. *dissecta*, and on this account it seems to be possible to give specific value to *S. Allionii*, though an experimental genetical investigation is desirable for a reliable decision.<sup>1</sup> *S. Allionii* must in any case be regarded as a comparatively old form, which indicates that the flax culture is of old date in Egypt (as is also known from archaeological finds). That it has not spread further (except occasional occurrences in late time) suggests that the flax culture, too, has not spread from Egypt to other countries.

*Cuscuta epilinum* is a flax weed which, as in the case of *Silene*

<sup>1</sup> Such investigations on the flax weeds seem, according to ROTHMALER (1946), to have been already begun in Germany.

*linicola*, has no self-evident close relationship to some parallel form. It is a good and independent species and it is doubtful what other species is most closely related to it. In the monograph of YUNCKER (1932) *C. epilinum* is referred to section *Eucuscuta*, subsect. *Europaeae*, a group of five species distinguished among other characters by sessile flowers, short styles and terete stigmas about as long as the styles. In ENGELMANN's monograph (1859), however, it is pointed out that the species may also be related to sect. *Epistigma*, which is distinguished by pedicellate flowers, but to which *C. epilinum* has a certain resemblance in the shortness of the styles as compared with the stigmas, a character that in sect. *Epistigma* is still more pronounced. At a closer investigation of the species belonging to sect. *Epistigma* it is however apparent that they have quite another flower type than *C. epilinum* (cf. Fig. 6 *h—k*) and the styles are also considerably shorter, almost undiscernable. There is apparently no closer affinity between *C. epilinum* and these species.

The species belonging to subsect. *Europaeae* show a greater similarity and an indubitably closer relationship to *C. epilinum*. A species of this section, the also geographically distant *C. madagascariensis*, differs, however, rather much in its long styles, styles and stigmas being together as long as the ovary, or longer (YUNCKER, 1932 p. 277). Another species, *C. palaestina* (Fig. 6 *l—n*) also differs in this character and its flowers are of another type, too, with spreading, cucullate corolla lobes etc. The remaining species are most closely related to *C. epilinum*: *C. europaea* and *C. kurdica*, near to it, both of which in the type of the flower approach closely *C. epilinum*. *C. europaea* is a polymorphous form of wide distribution, *C. kurdica* is a locally restricted species, probably arisen from *C. europaea*. In some deviations from *europaea* *C. kurdica* resembles *C. epilinum*, but in other respects it differs from it, as for instance in the smaller, generally tetramerous flowers and the slender styles and stigmas (Fig. 6 *o—q*). *C. kurdica* and *epilinum* appear not to have any direct genetical connection, their resemblance is probably due to the fact that both are closely related to *C. europaea*.

With *C. europaea* *C. epilinum* shows a great agreement in its general flower type (cf. Fig. 7 *a—j*). The main differences from *C. europaea* are that the flower as well as the ovary and fruit are broader in relation to their length, that styles and stigmas also are somewhat broader and shorter, that the corolla is more shallowly divided (to about  $\frac{1}{3}$ rd, in *europaea* to about  $\frac{1}{2}$ ), the calyx lobes acuter, the scales

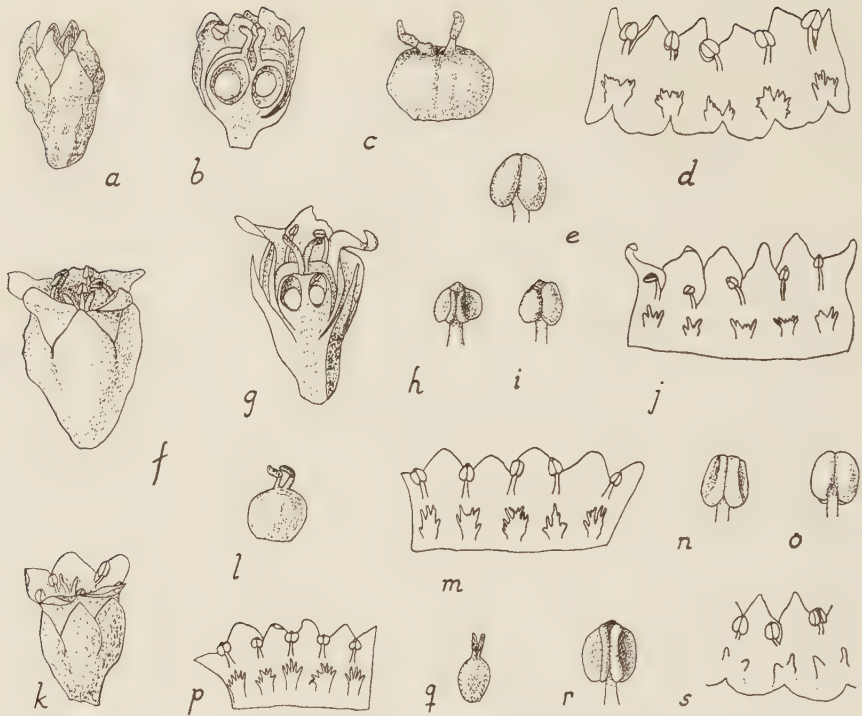


Fig. 7. a—e *Cuscuta epilinum*, flower in side view and in longitudinal section, pistil, corolla unrolled and anther; f—j *C. europaea*, flower from the side and sectioned, anthers and corolla; k—m *C. europaea* var. *indica*, flower, pistil and corolla; n—o anthers of *C. europaea* from Kashmir; Ladak; p—q corolla and pistil of *C. europaea*, somewhat deviating form from Bimgoell; r—s anther and part of corolla of *C. epilinum* from Persia, Bactiari. e, h—i, n—o, r  $\times 15$ , the others  $\times 5$ .

of the corolla tube larger, and the anthers larger and more oblong. In addition the seeds are larger, often united two and two, the fruits do not open regularly, and the stem is slightly branched. The latter characters may be entirely due to the selection in the flax cultures and the short and broad form of the flower and fruit may also be associated with selection of large-seeded forms under retention of a small diameter of the flower glomerules, the fruit agglomerations thus not much surpassing the flax fruits. The other differences may be due to the selection having started from a form of the polymorphous *C. europaea* having such or similar characters. As will be shown later on, there are some forms of this species that approach *C. epilinum*. First, however, an investigation should be made of the distribution of the two species.

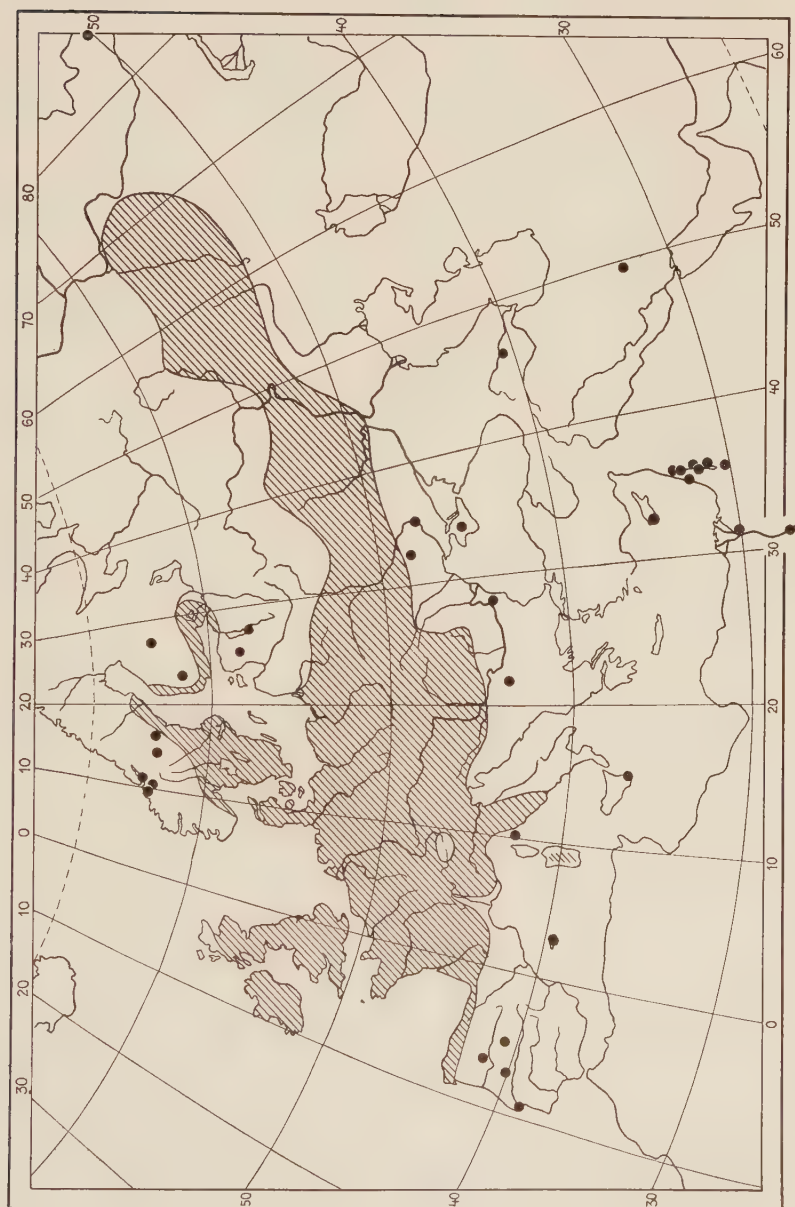


Fig. 8. Distribution of *Cuscuta epilinum*.



The distribution of *Cuscuta epilinum* is shown in the map Fig. 8. The species is mainly confined to Europe and apparently avoids the decided Mediterranean districts. In Azerbaijan (N. A. IVANOV, 1929) and in Persia (the Bachtliari district, BOISSIER, 1879, and herbarium material) there are further isolated occurrences, whereas the distribution in Siberia seems to be the result of a dispersal in recent times (GRJASEV, 1928; KHREBTOV, 1931). An introduction has also taken place into other more distant regions, for instance India (Calcutta) and North America (HEGI, 1927). Of great interest is, however, that in Palestine, Arabia Petraea and northern Egypt there is an isolated district with several localities (POST-DINSMORE, 1933, and MUSCHLER, 1912). As the localities are generally remote from the coast, partly in isolated districts, it does not seem to be a case of late introduction but rather of an old relict. To the same group belongs an occurrence at Cyprus, Kouklia (herb. mat.).

The distribution area of *C. europaea* partially coincides with that of *C. epilinum*, but extends farther especially to the east.

In northwestern Europe it has a more restricted area than the other species. From Ireland and Scotland it is scarcely recorded with certainty except as occasional (BENTHAM, 1866; WATSON, 1883; VERDCOURT, 1948) and in England it occurs in the most southern part only and reaches its northern boundary in the York district (WATSON, l.c.). In Norway (LID, 1944) it occurs mainly in the south-eastern part; besides there are some solitary localities farther to the west and the north, the most northern in Ørkedal. In Sweden the species reaches in the inland parts, though only occasional, to Jämtland (LANGE, 1938), whereas the northern limit in the coastal region passes through Medelpad (at Timrå and Skön). In Finland the distribution is wider than that of *C. epilinum* and extends over the southern part of the country to 63° north. lat. (HJELT, 1919). The geographical range of the species takes in the greater part of Russia (FEDTSCHENKO and FLEROV, 1910) and extends further through a great part of Siberia, as far as to the Lake Baikal and the river Wiljui (TRAUTVETTER, 1883).

In the south *C. europaea* extends into Southern Europe. In Spain it is only found in the northern and middle part (WILLKOMM-LANGE, 1870), not more southern than in the Madrid district. In Italy (PARLATORE, 1884—86) the species occurs over the greater part of the Peninsula; it is most spread in the northern part, but scattered occurrences are found through middle Italy and even as far to the south as in Basilicata (at about 41° lat.). From Sardinia and Sicily it is not reported, but it is found in Corsica (PARLATORE, l.c.). In the Balkan Peninsula the species occurs (HAYEK, 1931) in most districts, in the south to Greece, but is absent on the islands.

The distribution area is continued through West Asia into Central Asia. The species occurs here (according to herbarium material) in Asia Minor, even as far southwards as at Taurus, in Kurdistan, Armenia, Caucasia, Northern Persia, western Turkestan, Afghanistan, and reaches western Himalaya, where several collections have been made in Kashmir. It has also been found in Pamir (PAULSEN, 1906), in

western Tian-shan (BALABAJEV, 1925), Dzungaria (TRAUTVETTER, 1883), and Altai (LEDEBOUR, 1829).

The distribution areas of *C. europaea* and *C. epilinum* are thus to a great extent coincident, and with respect to distributional conditions many districts may be thought to be the native country of *C. epilinum*. It remains, then, to investigate whether there is some form of *C. europaea* that comes near to *C. epilinum* and forms a transition between the two species.

Two forms of *C. europaea*, *C. europaea* var. *Viciae* (KOCH, SCHNITZL. & SCHÖNH.) ENG. and *C. europaea* ssp. *halophyta* (FR.) HYL., have been stated by several authors to approach *C. epilinum*. About the former GANESHIN (1928), who regards it as a subspecies, says that in several respects it differs from *europaea* and resembles *epilinum*. Thus, the scales of the corolla tube were, in the material examined by this author, larger than in *C. europaea* and more richly fringed, the seeds are often united two and two, and the capsules open incompletely at maturity. However, other specimens investigated by the present writer, for instance from two localities in Bavaria, have not especially vigorous scales and are very reminiscent of the main form. That the seeds are sometimes double and the fruits open irregularly, may of course be a result of the selection in the vetch fields. It is a development that is parallel to that which has occurred in the flax crops, but owing to the inconsiderable difference between var. *Viciae* and the main form it has probably taken place in recent times and cannot have been of importance for the genesis of *C. epilinum*.

*C. europaea* ssp. *halophyta*, occurring in the Fenno-Scandian coastal regions, is more obviously different from *C. europaea*, as is pointed out more in detail by Finnish authors (EKLUND, 1928; KROHN, 1933). It is reminiscent of *C. epilinum* in its slight ramification, the generally 5-parted corolla, the broadly rounded corolla tube, etc. Contrary to *epilinum*, however, corolla and calyx are deeply divided, the calyx even more deeply than in *europaea*, almost to the base, and the stigmas are acute. Thus this form, too, apparently has no genetical connection with *C. epilinum*.

Another form that shows a certain resemblance to *C. epilinum* is *C. europaea* var. *indica* ENG. from the mountainous parts of Northern India. A collection of HOOKER f. and THOMSON with the locality Tibet Occidentalis, alt. 10—13,000 ft., is reminiscent of *C. epilinum* in the comparatively short flowers, the large and multidentate scales (Fig. 7 m), not very unlike those occurring in *epilinum* (Fig. 7 d), the more

or less erect corolla lobes (Fig. 7 *k*), the large anthers, yet apiculate, and perhaps also in the corolla being somewhat more shallowly divided than is usual in *europaea*. A collection of *C. europaea* from Afghanistan, Topchee (GRIFFITH, herb. Kew) shows in the comparatively large and multidentate scales some deviation in the same direction, though not so great. A collection from Kashmir, Ladak (KOELZ, 1931) agrees in most characters with *europaea*, but the anthers are large and without the apiculate top (Fig. 7 *n,o*); they are thus of the same type as in *epilinum* (Fig. 7 *e*). These agreements with *C. epilinum* seem to deserve attention; they refer to more or less important characters and are not accompanied by deviations in other respects as in the case of ssp. *halophyta*, but imply a real approach. In a biological respect also *C. europaea* can apparently in Central Asia approach *epilinum*; thus BALABAJEV (1925) reports that in a district of Tian-shan seeds of *C. europaea* occur mixed up in flax seeds; hence the species would here seem to grow as a parasite on flax.

In several places in the mountainous districts of Central Asia, thus, in *C. europaea* there occur different characters distinguishing *C. epilinum*; through combination of these characters and selection in the flax fields a form might appear that came near to *C. epilinum*. In the locality for *C. epilinum* in Persia, Bachtari, which is far advanced in this direction, this species moreover shows some features reminiscent of *C. europaea*, the scales being weakly developed and the anthers slightly apiculate (Fig. 7 *r, s*), characters that perhaps are not very important but nevertheless may have some significance; they are in agreement with a supposition that in these regions we have a transition from *europaea* to *epilinum*.

Regarding the fact that other flax weeds trace their origin from West Asia it would perhaps rather have been expected that *C. epilinum* had originated in a more western region (this is presumed by HELLWIG, 1886, and JESSEN and LIND, 1922—1923). In West Asia, however, there do not seem to exist any transitional forms between *C. europaea* and *epilinum*. There is no tendency in the direction of *epilinum* in the collections of *C. europaea* that have been examined by the author from this district (Asia Minor: Pontus, Sumila [SINTENIS, 1889 n. 1795], Taurus above Boulgarmaden [BALANSA, 1855]; Caucasus: Batum, Artwin [HOLMBERG n. 2294], Balkharia, Sukan [E. and N. BUSCH, 1925], Jugo-Ossetia, Zonskaja Kotlovina [E. and N. BUSCH, 1928]; Persia: Astara [COWAN & DARLINGTON, 1929], between Nischapur and Mesched [BUNGE, 1858]; prov. Musch: Bimgoell [KOTSCHY, 1859

n. 306]). The specimens are in general typical *C. europaea*; the last-mentioned number is somewhat deviating (Fig. 7 p, q) in the flowers being smaller and the scales larger than usual, but this difference is probably due to an approaching to *C. kurdica*, which grows in the same district, and not to *epilinum*. — Of the *C. epilinum* growing in the eastern Mediterranean region the author has seen specimens from Cyprus, Kouklia, only and these are in the essential characters typical *C. epilinum*.

Owing to the variation of *C. europaea* and *epilinum* it thus appears probable that the latter derives its origin from the mountainous districts in Central Asia and from there has migrated towards the west to West Asia and Europe, becoming more and more differentiated and pronounced. The distributional conditions suggest that a branch has then turned off towards Palestine and Egypt (probably comprising a more thermophilous ecotype), while the main stream has gone towards temperate Europe. In the common region of origin there are only scattered remnants left of *C. epilinum*, probably, as in the case of *Silene linicola*, due to the fact that it has not here become so differentiated that it has been able to vindicate itself with the same success as the more pronounced type in areas later reached.

Judging from the marked difference shown by *C. epilinum* from other species, implying that its specific rank cannot be called in question, it is doubtless an old species, one of the oldest flax weeds.

*Lolium remotum*, a flax weed with wide distribution, is closely allied to *L. temulentum*, and as early an investigator as ZINGER (1909) presumed that it had developed from this or from a common ancestral form under the conditions of flax cultures. It differs from *temulentum* mainly in being lower and more slender, more yellowish green in colour, more or less glabrous, the spikelets being smaller with smaller scales, the glume generally shorter than the spikelet (in *temulentum* longer), 5-nerved (in *temulentum* 7-9-nerved) and with broader scarious margin, the lemma generally awnless, the palea indistinctly veined and very slightly pilose in the margin (cf. Fig. 10 a and c with d). The characters are thus partly of a quantitative nature and within both *temulentum* and *remotum* there occur variants approaching the other species; among the varieties of *L. temulentum* mention should especially be made of var. *leptochaeton* A. BR. (= var. *arvense* [WITH.] BAB.) with reduced awn, and within *L. remotum* of var. *aristatum* (DÖLL) ASCH. with awned lemma; besides the pubescence varies in both



species independently of the occurrence of awns. Fig. 10 *b* in comparison with Fig. 10 *c* and *h* shows how near the deviating forms may come to each other. It is quite clear that the two species are closely related.

The geographical distribution also shows great resemblances. The distribution of *L. remotum* is shown in its main features in the map Fig. 9. Its northern limit is somewhat uncertain owing to changes in the flax cultivation. In the south it seems — like *Cuscuta epilinum* — to avoid the decided Mediterranean climate. Outside Europe it occurs in Caucasia, reaching the Caspian Sea (LEDEBOUR, 1853, and later authors) and is reported by BALABAJEV (1925) from western Tian-shan, the Tashkent district; the locality is perhaps identical with LEDEBOUR's »Turcomannia» (l.c.).

*L. temulentum* has a distribution much resembling that of *L. remotum*, but it is considerably more extended towards the south and south-east.

In the British Isles it occurs over the greater part, save only northernmost Scotland (WATSON, 1852; DRUCE, 1932). In Scandinavia it is known as far in the north as in North-Trøndelag in Norway (LID, 1944) and Norrbotten in Sweden, but the most northern localities are to be regarded as occasional and as more permanent it is found only in southern and western Scandinavia (HOLMBERG, 1926). In Russia the limit is roughly parallel to that of *L. remotum*, but it runs somewhat inside of it (MALZEV, 1910, map). In the south the species occurs also in South Europe and Asia Minor (here abundantly in the coastal regions, SCHEIBE, 1935) and in North Africa (BOISSIER, 1884; and other sources). In West Asia it occurs over large areas as far as to Afghanistan in the east (BOISSIER, l.c.).

For a derivation of *L. remotum* it is of importance to investigate the occurrence of transitional forms to *L. temulentum* (or possibly some other species). The above-mentioned var. *leptochaeton* and var. *aristatum* occur here and there within the area of *L. temulentum* and *remotum* respectively, though it is stated from Russia that *L. temulentum* var. *leptochaeton* is there restricted to the districts at the Black Sea and Caucasia (NEVSKI in KOMAROV, 1934). These forms however retain the characters of the main species in, for instance, the number of nerves and the scarious margin of the glume and var. *leptochaeton* is perhaps rather a parallel form developed in corn fields than a transitional form to *remotum*. In West Asia there is to be found, however, a form akin to *temulentum*, viz. *L. persicum*, which in the characters mentioned of the glume approaches *remotum* (Fig. 10 *f*). This species occurs (NEVSKI in KOMAROV, 1934) in Caucasia, Armenia, Kurdistan, Persia, West Turkestan, Pamir-Alai, Tian-shan. It has glumes that are

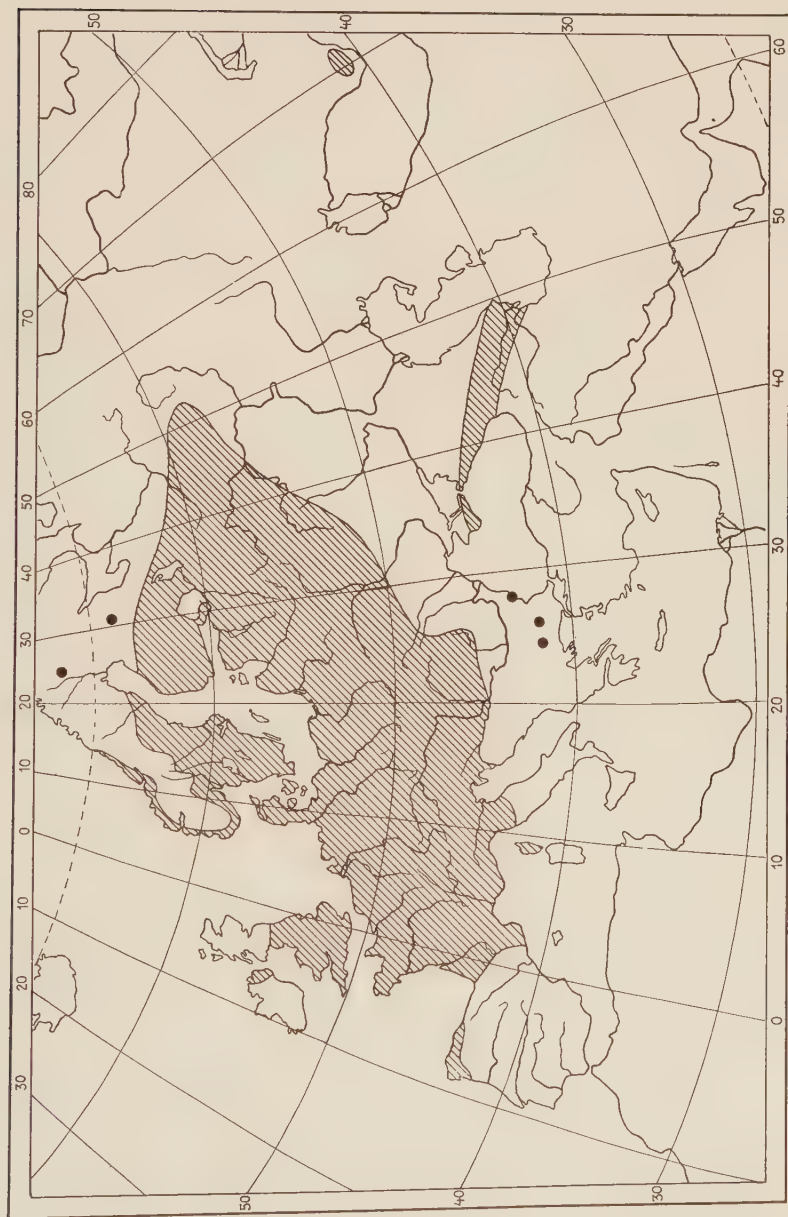


Fig. 9. Distribution of *Lolium remotum*.

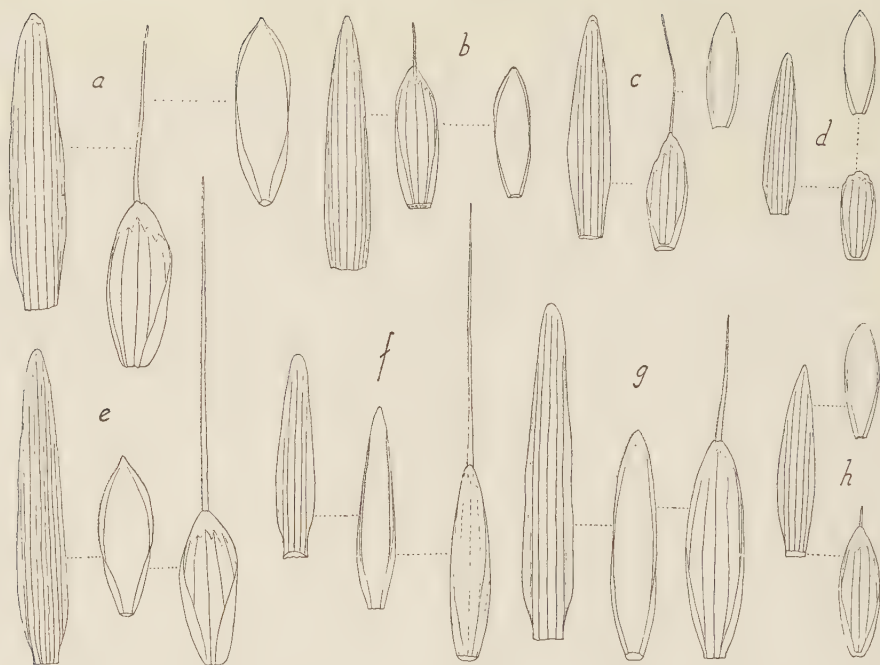


Fig. 10. *a* *Lolium temulentum* from Cyprus; *b* *L. temulentum* var. *leptochaeton* from Membidj at Euphrates; *c* *L. remotum* var. *aristatum* from Saxony, Schlieben; *d* *L. remotum* from Galicia; *e* *L. temulentum* from Transcaspia, Kisil-Arwat; *f* *L. persicum* from Elburs; *g* *L. temulentum* from Armenia, near Goel, form approaching *persicum*; *h* *L. remotum* from Bohemia. Of each form the glume is figured, the lemma from the inside and the palea from the axis.  $\times 3$ .

shorter than the spikelets, 5-nerved and with comparatively broad scarious margin. The awn is thin and slender. The flower-scales are however long and narrow, differing both from *temulentum* and *remotum*, perhaps most from the former. Transitional forms between *temulentum* and *persicum* seem also to exist, as the one pictured in Fig. 10 *g* (from Turkish Armenia, near Goel), a form of *temulentum* that in the narrow flower-scales and also in the glume apparently approaches *persicum*. On the whole, the *L. temulentum* group varies much in the uplands of West Asia; by NEVSKI there are from here listed five species of the group: *remotum*, *temulentum*, *arvense* (by him regarded as species), *persicum* and *cuneatum* NEVSKI, and the abundance of forms is so great that *L. remotum* may very well have had its point of origin here, a further development then taking place by way of selection in

the flax fields. That *L. temulentum* here also, rather far to the south-east, has characters reminiscent of *L. remotum* is evident from Fig. 10 *b*, which figures a specimen from Membidj at Euphrates. The most probable origin for *L. remotum* is apparently *L. temulentum* in a form somewhat approaching *L. persicum* (though not just such a one as is reproduced in Fig. 10 *g*), and the most probable countries of origin are the uplands of Armenia, Caucasia, and northern Persia.

Another flax weed of the genus *Lolium* is *L. brasilianum* NEES. This species is described from South America, Uruguay, by NEES VON ESENBECK (1829) and quite recently it has been established by ROTHMALER (1944) that it is also found in Portugal, principally as weed in summer and winter flax, exceptionally in rye and other crops. It is closely allied to *L. multiflorum* and differs from it (ROTHMALER, 1944, 1946) mainly in being always annual, subglabrous, with smaller spikelets, only 5—8-flowered, the glume being shorter and broader, 5-nerved (in *multiflorum* 7-nerved), obtuse and with broader scarious margin. The flower scales are also shorter than in *multiflorum*, the seeds smaller. ROTHMALER supposes that it has arisen by way of selection in the flax fields of the Iberian Peninsula and has from here spread to South America. This mode of origin is of course highly probable in view of the characters, which are very reminiscent of those distinguishing *L. remotum* from *temulentum*. Judging from the herbarium specimens of ROTHMALER, as well as his statements, the differences from *multiflorum* are however by no means so distinct as these of *remotum* from *temulentum*. *L. multiflorum* shows a great variation, for instance in the development of the glumes, and often approaches *brasilianum* without any sharp limit. The latter is on this account probably a flax weed which has arisen in comparatively late times.

*Lepidium sativum* L. is a species that often occurs as a flax weed in the Mediterranean region, for instance in Egypt (THELLUNG, 1928), Greece and Albania (BERTSCH, 1947), Sardinia (PARLATORE, 1890—1893), and also in Abyssinia (SINSKAJA, 1931). THELLUNG (1928) distinguished two spontaneous forms, var. *silvestre* THELL. and ssp. *spinescens* (DC.) THELL., which occur in North Africa and Southwest Asia from Kordofan and Abyssinia to the Himalayas, and on the other hand the cultivated form var. *vulgare* SPENN. The flax weed is according to him identical with the cultivated form and he is of the opinion that this form has developed as a flax weed. This is supported by the fact that the species has quite different names among different peoples, which may happen in the case of a weed but is unusual in the case of



a culture-plant that is spread from people to people, and the weed and culture plant have larger seeds than the wild-forms, which may be explained by selection in the flax fields but scarcely by the culture, which does not generally aim at the seeds. There are however also, in the opinion of the present writer, some facts arguing that the culture form is the primary one and that the flax weed has arisen by naturalization of this, as actually is often the case. Firstly, the weed plant often grows in other habitats than flax fields, gardens *etc.* Further, according to another work by THELLUNG (1907) there are archaeological finds from Egypt that belong to var. *silvestre* and this small-seeded type thus seems to have been taken into cultivation in ancient times. According to DECANDOLLE (1883), the species was also formerly cultivated for the sake of the seeds, as is still the case in for instance Abyssinia (THELLUNG, 1928), and the seed size may thus have increased during cultivation. Investigations in Abyssinia (SINSKAJA, 1931, after SHTCHENKOVA) have further shown that the flax weed is not here identical with the culture-plant; it differs (f. *linicola*) from it in having larger seeds. This suggests that the flax weed has arisen through naturalization from the culture. To the difference of names among different peoples it may perhaps not be attached such a great importance; the names of garden plants seem to change more than those of agricultural plants. The cultivated form thus appears to be the primary. That the deviations from this, if at all present, are so small, indicates that the spreading from the culture to the flax fields has taken place in recent times.

A parallel to *Lepidium sativum* is to a certain degree formed by *Eruca sativa*. This species also occurs both as flax weed and as cultivated, spread over the Mediterranean region, South Russia, West Asia, India, and also China (SINSKAJA, 1925). In the flax fields there occurs a form with short and orbiculate fruits (SINSKAJA, 1928). With regard to this species, too, it has been presumed that the culture-plant derives its origin from the flax weed; in some districts (Asia Minor, SERDYUKOV, 1931, according to ZHUKOVSKIJ; Bokhara and Turkestan, SINSKAJA, 1925) it has actually been observed that under suitable conditions it has passed from admixture to flax (for oil) to independent culture plant. It is however to be observed that at least in India (WATT, 1908) *Eruca* is often cultivated in mixtures with other plants, just as the flax is often mixed with other oil plants; of course it then easily happens that through external conditions the one or the other plant in these mixed cultures becomes dominant, just as at such a culture a species is easily mixed up as a weed in another crop. In this case, too, the

writer inclines to the opinion that the culture plant is primary and that the flax weed has arisen through naturalization of this in different parts of the cultivation district, a development that has probably taken place in recent time, since no pronounced weed forms have become differentiated.

In East Europe there occur a couple of specialized flax weeds of limited distribution. The one is *Agrostemma linicola*, which is found in central Russia in the Volga and Don districts (TERECHEV, 1931; KOMAROV, 1936). It was described by TERECHOV (1931) and differs according to him from *A. githago* in the seeds being considerably smaller, only slightly tuberculate on the surface, the calyx tube narrower and less hairy. It is a summer annual, which however is generally also the case with *A. githago* in East Europe. The species is little known (cf. KOMAROV, 1936) and has not been seen by the author. The other species is *Polygonum linicola* SUTULOV, also occurring in central East Europe, yet with a wider distribution, from Esthonia in the West (NENJUKOW, 1927) to the Vyatka district in the East (KOLOKOLNIKOV, 1931) and occasionally outside this area (NENJUKOV, *l.c.*). It is closely related to *P. lapathifolium* and differs from this mainly in the non-articulate pedicels and the larger fruits, somewhat extruding from the perianth (cf. NENJUKOW, *l.c.*; THELLUNG, 1930); owing to the small difference DANSER (1921) doubts, rightly, its specific value and regards it as a subspecies, ssp. *leptocladum*. — Both these forms have doubtless arisen by way of selection in flax fields, but they are certainly to be regarded as forms that have arisen in recent times and that have a locally restricted distribution.

Still some other plants are reported to be special flax weeds. From Transcaucasia it is thus stated (SERDYUKOV, 1931) that *Lallemantia iberica* and *peltata* and *Chaerophyllum bulbosum* are there »*plantae linicolae*». Even if these plants occur in great abundance in flax fields and especially the *Lallemantia* species in their seed size, *etc.* are well fitted for this, they also occur, in the same form, at other habitats and can thus scarcely be considered as special flax weeds. There is apparently, then, more reason for referring *Galium spurium* to them, according to for instance NENJUKOW (1927). This species occurs in the flax fields in East Europe *etc.* and differs from the forms related to it, *inter alia*, in the glabrous, adherent fruits, a character that of course may have arisen by way of selection in the flax fields. The species, however, also often occurs in other vegetation (cf. for instance HAYEK, 1912); thus, it is uncertain whether it is a specialized flax weed proper.

*Alopecurus agrestis*, too, occurring in the flax fields of north-western Europe (cf. HEGI, 1924—1925), is not restricted to flax fields, but is also found in many other habitats, and *Lolium westerwoldicum* or *L. italicum* var. *westerwoldicum*, which is sometimes recorded as a flax weed in North-west Europe (HEGI, 1924—1925; ROTHMALER, 1944), seems to be a form that has never been described and has a doubtful systematical value.

### Discussion and conclusions.

Some of the flax weeds treated above are slightly deviating forms of locally restricted distribution, which obviously have arisen in recent times, as *Silene gallica* var. *linophila*, *Lolium brasilianum*, *Agrostemma linicola*, and *Polygonum lapathifolium* ssp. *leptocladum*. Another group has probably arisen through naturalization of cultivated plants in late time (*Lepidium sativum*, *Eruca sativa*). A third group comprises forms with a wider distribution and generally more pronounced characters. These are of the greatest importance for the question of the origin of flax. In many cases they clearly show an ever stronger differentiation towards the northern and western part of their area of distribution, indicating an immigration from south-east to the north and west. This is true both of the more slightly different, and thus probably younger, weed forms within *Camelina* and *Spergula* and the more pronounced flax weeds within *Silene* and *Cuscuta* and may be taken as evidence that the spreading of the flax culture has gone in the same direction (on the whole from south-east to north-west). A further fact of importance for the question of the origin of flax is that those flax weeds which, with regard to their independent systematical position, appear to be the oldest in general point to Asia as their native country. *Silene linicola* certainly derives its origin from the district in Syria and Palestine where *S. crassipes* occurs, probably its northern part, and *Lolium remotum* probably from an adjacent, though somewhat more northern, district, *Cuscuta epilinum* from a more eastern Asiatic territory. For the flax weeds belonging to *Silene cretica* matters stand somewhat different. Their first origin is probably localized to the eastern Mediterranean region, Crete-Cyprus or neighbouring districts. This is not very remote from, for instance, the country of origin of *Silene linicola*, but the immigration has nevertheless followed different routes. The *Silene cretica* forms have spread through the Mediterranean region and from there found their way up to more northern districts, even — in pre-historic time — to the district of the lake-dwellings in

Switzerland. *Silene linicola*, *Lolium remotum*, and *Cuscuta epilinum* on the other hand must, as is shown by still present or earlier occurrences, have migrated over the northern Balkan Peninsula and the Danubian countries, thus arriving into Europe more from the east. These two different paths of migration are in agreement with the assumption (cf. BERTSCH, 1947) that flax has been introduced into central Europe on one hand from the Mediterranean region, as was already supposed by HEER (1872), on the other hand from the east, the old Danubians (*Bandkeramiker*) apparently having brought about the introduction. The flax that has come from the Mediterranean in a northern direction must derive its origin from the *Linum angustifolium* growing here, as was already assumed by HEER owing to the great similarities between this species and the flax of the lake dwellings in important characters. For the flax introduced into Europe from the east the origin can be the same species, viz. if the country of origin is not farther to the east than in the district where *Silene linicola* and probably also *Lolium remotum* have originated; here *Linum angustifolium* is also found as spontaneous (to western Persia in the east). There are however, as was stated above, certain reasons arguing in favour of the view that *Cuscuta epilinum* has a more eastern country of origin, probably in Central Asia; if this should be true also of the flax, the ancestral species must be a different one. It is not possible to draw any extensive conclusions from the history of a single weed. It should however be pointed out that *C. epilinum*, judging from its variation and other circumstances, has probably spread from the east to the west and that, in view of its independent position, it probably belongs to the oldest flax weeds of all. It is also to be observed that according to several authors the species does not parasitize *Linum angustifolium* (a contrary statement by MORIS, 1858—1859, possibly refers to an exceptional case). On this account, the possibility cannot be quite left out of consideration that the cultivated flax has arisen in Central Asia and on its way towards the west in the old countries of high cultivation, where it has been grown intensely, has caught up new special flax weeds. In this connection it should be pointed out that VAVILOV (1926) has established a centre of diversity for the flax in the mountainous districts of Afghanistan and surrounding regions and further that CHEVALIER (1944) is of the opinion that the Central-Asiatic *Linum perenne* may have contributed to the genesis of cultivated flax (cf. also WATT, 1908); of this species there is also an annual or biennial form that shows great resemblance to *Linum usitatissimum* and the species,



as a matter of fact, has actually occurred in cultivation. — A difficulty in the way of such a presumption is the fact that *Linum perenne*, as far as known, has a different chromosome number from *L. usitatissimum* (18 as against 30—32, SCHIEMANN, 1932; according to RAY, 1944, the number of *L. usitatissimum* is 30); it is however perhaps imaginable that different forms of the polymorphous *L. perenne* have different chromosome numbers.

The special flax weeds cannot supply any definite answer to the question of the ancestral species of cultivated flax; this is a question that in the first place must be decided by investigations of the flax itself and the wild forms related to it. The history of the flax weeds however contributes some guidance to the solution of the question concerning the origin of cultivated flax. It indicates that the flax in Central Europe has immigrated from the south and the east, that it has had two different paths of migration and that it derives its origin, on the one hand, from the Mediterranean region, probably its eastern part, on the other hand, from a more eastern, Asiatic, region and it suggests as a possibility, worthy of further investigations, that in the mountainous regions of Central Asia there may exist a wild form from which the cultivated flax in part may derive its origin.

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## Radiation of Desmids,

its origin and its consequences as regards taxonomy and nomenclature.

By EINAR TEILING.

Among all non-sphaerical organisms, the desmids take up an unique position because of their polysymmetric structure. A desmid is symmetrical with regard to a plane passing through the isthmus and perpendicular to the vertical axis, and, if not cylindrical, they show, in end view diverse forms which agree with certain fundamental geometrical forms; elliptic, triangular, quadrangular or polygonal. The corners are often rounded but sometimes, especially in triangular-polygonal desmids, extended into solid or hollow processes. These protruding parts are named rays (*radii*) which has given rise to the term radiation, not previously used in this sense.

Radiation means that element of structure which is decisive in the shape of the desmids according to their vertical symmetry-planes. The number of the corners is dependent on the number of the symmetry-planes through the vertical axis. In the following only those radiation-planes passing through the vertical axis are dealt with, since the isthmal plane is common to all desmids. When discussing the radiation it is convenient to use special terms. The shape of a semicell which is circular in end view (*a vertice*), is named *omniradiata* as a contrast to the *anguloradiata* forms. Of the latter it is convenient to distinguish between *biradiata* and *pluriradiata* (TEILING 1948). Within the pluriradiata forms there are such ones with three, four, five and up to about a dozen corners. The terms are: *triradiata*, *quadriradiata*, *quinque-radiata* and so on, the radiations 5—12 are summed up as *polyradiata*. When written, the radiations are conveniently indicated by figures, especially the more uncommon; 4-, 5-, 6-, etc. radiation. A species, known as appearing in two or more radiations, is said to be *dimorphic* etc. When several radiations on the whole are known in a specimen, this is called *pleoradiation*.

A specimen having two perpendicular vertical planes, in end view forming the axes of an ellipse, is biradiate (f 6—9, 15). Most species of *Staurastrum* possess three or more vertical symmetry-planes always parting the circle in equal parts (f 11—14). The semicell shows a correspondingly angular shape *a vertice* and is, according to the number of the corners, triradiate, 4-radiate and so on. It must be pointed out, that the radiation must not be uncritically identified with the rays, a term often used in the literature in order to signify processes in general. The »rays» (=processes) of *Staurastrum Arctiscon*, for example are 15 in number (f 18), this desmid is not 15-radiate, neither is *St. barbaricum* 6-radiate; both are triradiate. Confusion may be produced by expressions like this »vertical view triangular (or up to 9-radiate)» in WEST, Monograph V, p 189. The actual desmid, *St. furcigerum* is triradiate, but the three processes each bear one or two accessory processes.

It is a remarkable fact that the radiation, though used as an important taxonomical character, has not been the subject of elucidation even in review papers on desmids; RABENHORST (1865), KIRCHNER (1878, DE WILDEMAN (1896), KRIEGER (1937), PRINTZ (1927), IRÉNÉE-MARIE (1939) do not mention it. OLTMANNS says (1922, p 107): »In Gegensatz zu diesen beiden Gattungen (*Cosmarium* und *Euastrum*) ist das ebenfalls eingeschnürte *Staurastrum* von der Frontseite beobachtet, sternförmig» (Frontseite» is a mistake for »Scheitelseite»). The WESTS, in Monograph I, p 4, have only the following words: »Seen from the vertical view, many exhibit a radiating structure, the number of radii varying from three to ten». FRITSCH (1927, p 253) mentions *Staurastrum* as having »a radiate character with 2-, 3-, 4-, or more-angled end-views, the corners being often drawn out into long processes». The WESTS have in discussions on several *Staurastrum* and *Arthrodesmi* considered the radiation as a phylogenetic principle and invariably emphasized that pluriradiate types derive from biradiate.

The author has for a long time devoted his attention to this neglected feature of the desmids and wishes to give a survey of the results obtained from the literature available to him, and from his own research, and, further, to relate them to some of the fundamental problems in Desmidiology. At last the author submits a theory of the origin and development of radiation, and a proposal of expressing the radiate features nomenclatorically.

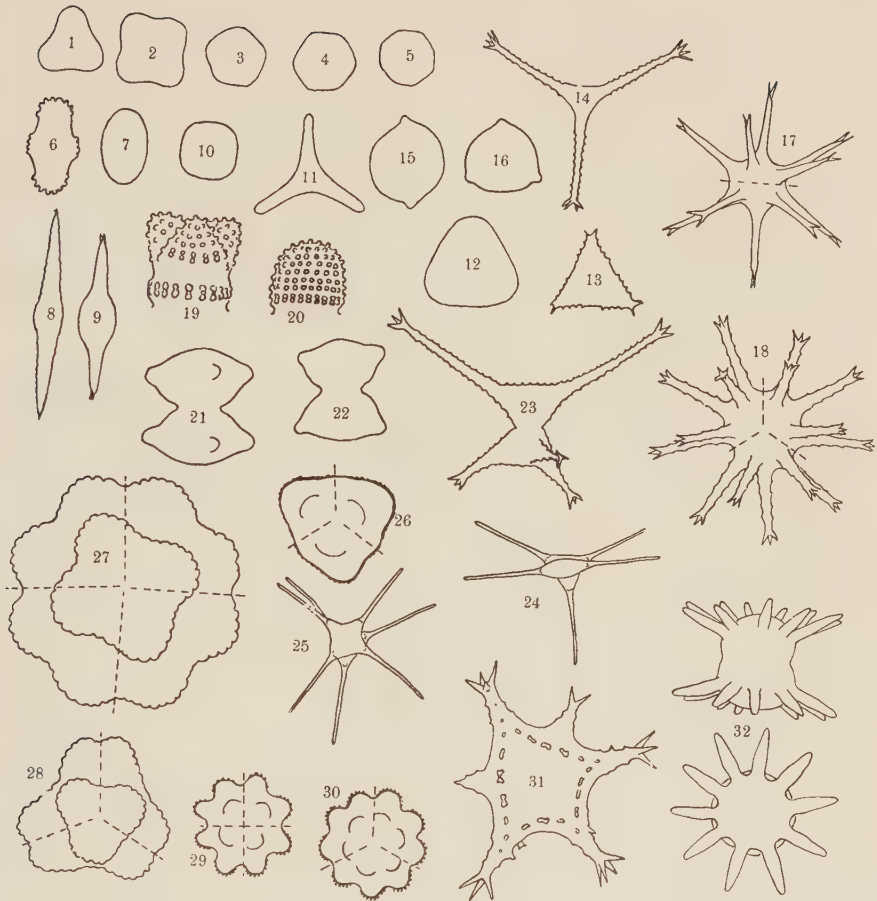


Fig. 1—5: *Staurastrum Merianii*, 6: *Cosmarium commissurale*, 7: *C. contractum*, 8: *Micrasterias* Sol, 9: *St. Duacense*, 10: *St. inflatum*, 11: *St. laevispinum*, 12: *St. orbiculare*, 13: *St. polymorphum*, 14: *St. longipes*, 15: *Hyalotheca dissiliens* f. *bidentula*, 16: same sp. f. *tridentula*, 17: *St. leptacanthum*, 18: *St. Arctiscon*, 19: *St. pileolatum*, 20: *C. pseudamoenum*, 21: *St. subpygmaeum*, 22: *C. capitulum*, var. *groenlandicum*, 23: *St. Chaetoceras* Janus (2 + 3), 24: *St. triangularis* Janus (2 + 3), 25: same sp. Janus (3 + 4), 26: *Euastrum pingue* var. *triquetrum*, 27: *Euastridium Prainii*, 28: *Eud. staurastroides*, 29: *Eud. verrucosum*, 30: *Eud. polonicum*, 31: *St. anatinum*, 32: *St. Victoriae*. — (1—4, 6—14, 21, 22, 27, 32 after WEST, 5 after BECK-MANNAGETTA, 15—16 after BOURRELLY, 17 after G. M. SMITH, 18 after LUNDELL, 28 after N. CARTER, 29 after PRESCOTT, 30 after DICK, 23—25, 31 orig., 19 after LÜTKEMÜLLER, 20 after NORDSTEDT, 26 after GRÖNBLAD. — The dotted lines in the figures 17, 18, 26—30 indicate the limits of the corner-regions.



### The occurrence of the radiation in some prominent genera.

The varied radiation implies a distinct difference of the shape of the semicell, especially in end view. Thus, in the early days of Desmidiology it was supposed that the radiation was a constant character and this concept has exerted an influence on taxonomy which can be traced through the whole history on Desmidiology. Genera were created on the basis of radiation, which in these cases has been overestimated, on the other side, the varying radiation within a clearly distinguished species in higher radiations has been generally neglected. As normal the radiation of a species was comprehended, which was found on the original specimen by the Auctor. A classical example is seen in *Staurastrum* (=cross-star), created on the basis of one (?) 4-radiate specimen, laconically mentioned in 5 lines under the name *St. paradoxum* (MEYEN 1829). When afterwards similar, but pluriradiate desmids were found the genus-name *Phycastrum* was proposed by KÜTZING 1845. This name was, with respect to the priority, refused by RALFS 1849, who, however, was quite aware of its greater expediency. Even, there was delivered a short-lived proposal of names, by HASSAL 1845, giving expression to the diverse radiations within *Staurastrum*.

Now we know a great number of pleoradiate species within almost all anguloradiate genera. The mutual connection of these species, at least of the pluriradiations, is easily recognized by means of morphological similarities. Sometimes, however, very clear connections are not made, if the one desmid previously is labelled *Cosmarium* or *Arthrodesmus* and the other is known as a *Staurastrum*. It is a peculiar fact, interesting from a psychological point of view, that desmidiologists easily unite specimens of, for instance, 3—6-radiate shape, but have been unable to identify as identical specimens of very similar shape, if bi- and triradiate. Thus, there has been created an imaginary cleft, still existing between *Cosmarium* - *Arthrodesmus* on one side and *Staurastrum*, on the other.

The forms, deviating from the species described as typical, are given names of *varietas*- or *forma*-status, for instance *Cosmarium amplum* f. *trigona*, *Euastrum pectinatum* var. *brachylobum* f. *triquetra*, *Micrasterias Murrayi* var. *triquetra*, *Xanthidium antilopaeum* var. *triquetrum*. In a sharp contrast to all this giving of names to these tri-radiate forms stands the slight interest, devoted to the pluriradiate, more pleoradiate species, the variation of which, however, is of the same scientific importance. The diverse 3—9-radiate forms of *Staur-*

*astrum margaritaceum* are hardly attended to, for they belong to a pluriradiate species. This is a rudimentary form of comprehension from a time when each little foot-bridge over the cleft between the bi- and pluriradiate genera was of special interest.

Most of the very oldest known species are omniradiate or biradiate except *Desmidium*. A simple survey of the species of RALFS's British Desmidiaceae shows that it contains 46 »cylindrical», 76 »compressed» and 42 »angular» species. RABENHORST's more extensive Flora (1868) contains 93, 143 and 68 species respectively. Thus, *Staurastrum* was adopted as a convenient label for all the pluriradiate desmids found. To the single species *Staurastrum paradoxum* there has been agglutinated about 600 species, an immense and extremely heterogeneous *omnium gatherum*, comprising many important generic divisions, several of which having nothing common with the *paradoxum*-core apart from their pluriradiate structure. Many of the species, allied to the *paradoxum*-type, are biradiate and are, quite rightly, placed in *Staurastrum* in spite of their biradiate structure.

Desmid-research has, especially during the last 80 years, resulted in the description of thousands of forms which, with few exceptions have been placed in the classical genera, often without considering their provisional character, especially is this the case for *Cosmarium* and *Staurastrum*.

A survey of the distribution of the radiation in the desmids will be demonstrated in the schema, p 304. The genera are placed in columns indicating the radiation with a convenient generalisation. The disposal of genera is not meant to intimate any degree of evolution.

A survey of the radiation within *Staurastrum* may be of interest. The author has chosen the *Staurastrum* of the British Islands, being the best examined, clearly delimited area of the world, as described in the monograph of W. and G. S. WEST and N. CARTER. The species belonging to *Staurodesmus* are excluded.

Within the material considered, species are found with all radiations from 2- up to and including 10-radiate. Table I, combined with table II, shows that the radiations of higher rank, 6—10, occur very rarely and always linked to adjacent radiations. *St. margaritaceum* is found in seven radiations. Quinqueradiate specimens are not uncommon, occurring in 24 species but no one is known as exclusively 5-radiate. Among the 4-radiate 7 are known exclusively as 4-radiate, but 64 species more may take on a 4-radiate shape. The maximum of *Staurastrum*-forms, viz. 158, appears as triradiate but only 88 of these are

Omniradiate	12—5-radiate	4-radiate	3-radiate	2-radiate
				<i>Micrasterias</i>
			<i>Euastridium</i>	<i>Euastrum</i>
				<i>Xanthidium</i>
				<i>Oocardium</i>
				<i>Cosmocladium</i>
				<i>Onychonema</i>
	»Cos- -marius»			
				<i>Spondylosium</i>
				<i>Sphaerosoma</i>
				<i>Hyalotheca</i>
		<i>Phymatodocis</i>	<i>Streptonema; Bambusina</i>	
			<i>D e s m i d i u m</i>	
		<i>S t a u r o d e s m u s</i>		
				»Arthrodesmus»
<i>Pleurotaenium</i>		»S t a u r a s t r u m»		
<i>Closterium</i>			<i>T r i p l o c e r a s</i>	
<i>Docidium</i>			<i>Triplastrum</i>	<i>Ichtyocercus</i>
<i>Penium</i>				<i>Tetmemorus</i>
<i>Saccodermæ</i>				

»constant». The biradiate shape occurs in 32 species, 11 are »constant». It should be noted that the numbers of species with »constant» radiations, are maximum-numbers, many of the desmids, hitherto known only in one radiation, will be found to be pleoradiate.

Table II shows the number of species, known to appear in one, two, three and so on radiations, without regard to the extent of variation, noted for the species. More than half the number of species, 58 %, are »constant». Together with the bi- and trimorphic species they include 96 % of the whole material; only 4 % are varying within 4—7 radiations with an evident decrease in the direction of higher ranks.

Table III shows the number of species which are known in possibly

Table I.

amplitude of radiation	number of species	% of 185
x = 2	11	6
3	88	48
2-3	12	6,5
4	7	3,5
2-4	7	3,5
3-4	33	18
2-5	2	1
3-5	12	6,5
4-5	4	2
3-6	2	1
4-6	1	0,5
3-7	1	0,5
4-8	1	0,5
3-9	1	0,5
4-9	1	0,5
8-10	1	0,5
9-10	1	0,5
	185	100

Table II.

found varying in x diverse radiations	number of species	% of 185
x = 1	106	58
2	50	27
3	21	11
4	4	2
5	2	1
6	1	0,5
7	1	0,5
	185	100

Table III.

found as x-radiate	number of species	% of 185
x = 2	32	17
3	158	90
4	71	38
5	24	12,5
6	7	4
7	4	2
8	4	2
9	4	2
10	2	1

Table IV.

radiation	found in species which show radiations, extended over the following radiations	amplitude of extended radiations
2	2-5	4
3	2-9	8
4	2-9	8
5	2-9	8
6	3-9	7
7	3-9	7
8	4-10	7
9	3-10	8
10	8-10	3

2-, 3-, and so on radiate shape. About 90 % of the British *Staurastrum* may be found in the triradiate shape and 38 % in the 4-radiate shape. With increasing radiation there is a rapid fall in the percentage.

Table IV shows in which combinations a radiation may occur and the extent of the amplitude within which the actual radiation is situated. The ends of the series are the smallest but, as a whole, there is a remarkable uniformity in the possibilities.



It is conceivable that this survey, founded on carefully examined material, is applicable to the *Staurastrum* in general.

Of *Cosmarium* to which all biradiate non-colonial desmids without deeper incisions and processes are reckoned, FRITSCH already in 1933 could mention 22 dimorphic species. Even in more constantly biradiate genera there occur dimorphic species: *Micrasterias* possesses 4, *Euastrum* 5 and *Xanthidium* 5.

Sometimes the radiation is not immediately discernible. In such cases the starting-point is, that the corners are congruent. The corners may be vague if they are divided up into several processes, the arrangement of which, however, is congruent: an examination always unveils the real shape of the corners, even if one or other of the processes may be reduced and lacking. Earlier, p 300, it has been stated that *Staurastrum Arctiscon* is triradiate. Seen in end view the 15 processes are arranged in three groups, each composed of two apical processes and three basal ones. Each group implies one corner, a structure-radius, fig 18. The body of the semicell is subsphaerical, a result of the close arrangement of the processes; in order to get the best common exposure to the light, the substrate must be sphaerical. In *St. Tohopekaligense* and similar forms with groups, consisting of 1+2 processes, the risk of mutual shadowing is smaller; accordingly the semicells form clearly protruding corners. *St. leptacanthum* possesses four apical and six basal processes, their arrangement shows that they form two groups of 2+3 processes, identical with those of *Arctiscon*; *St. leptacanthum* is biradiate (f 17). It seems likely that desmids described as *St. Arctiscon* var. *glabrum* actually are triradiate forms of *St. leptacanthum*, the length and apical forks of the processes being no specific characters. The subsphaerical semicells of *Staurastrum Löfgrenii* BORGE, examined *a vertice* in a similar manner, shows a 6-radiation: each corner is well characterized by a group of 1+2 spines, arranged as in *St. Tohopekaligense*. These are only a few examples of the use of a method, which facilitates the discerning of the radiation in intricate cases.

*Bambusina*<sup>1</sup> seems to be apprehended an omniradiate genus: »vertical view circular, often with two opposite mamillae» (WEST-CARTER, Monogr. V, p 155). There is, however, found a var. *trigona* (SCHRÖDER 1896, p 29, t I: 8) with three equidistant mammillas. This genus must be regarded bi- and triradiate, the mammillas being rudi-

<sup>1</sup> According to the International Rules of Botanical Nomenclature 1912, p 74, *Bambusina* is a *nomen conservandum* and *Gymnozyga* a *nomen rejiciendum*.

ments of the corners. In *Hyalotheca*, at least *H. dissiliens* (f 15, 16) the same traces of radii have been known for a long time (NORDSTEDT 1873). From the supposition that *H. dissiliens* is genetically allied to the other species, the genus *Hyalotheca* must be regarded as bi- and triradiate in spite of its circular shape in end view. *Bambusina* and *Hyalotheca* are examples of *pseudo-omniradiation*. This phenomenon is not confined to the filamentous desmids, an excellent example is *Cosmarium Welwitschii* W. et G. S. WEST. In the quite circular end-view of the subsphaerical semicell the biradiation is distinctly marked by two rows of verrucae.

### Applications of the concept of radiation to some taxonomical questions.

The earliest desmidiologists established a lot of genera not uncommonly on the basis of a single species, most of them abandoned and forgotten. New species were joined to these genera, from our present point of view, in many cases, by a mere chance; the genera then being quite diffuse. In 1840 MENECHINI in his Synopsis brought together the desmids, then known, into five principal genera: the filamentous ones into *Desmidium*, the elongated ones into *Closterium*, the flattened and lacinate ones into *Micrasterias*, the compact ones into *Cosmarium* (including *Euastrum* and *Xanthidium*) all of them biradiate, the brachiate (pluriradiate) and spinous (bi- and triradiate) into *Staurostrum* (including *Arthrodesmus*). This system was by RALFS (1849) revised and improved to form his standard-work. In this however, the fictive cleft between *Cosmarium* and *Staurostrum* was codified. The visual contrast between bi- and triradiate desmids is very striking, more obvious than between other radiations. From a practical point of view this bipartition of the desmids is justified, but it is artificial, quite in the same way as the sexual system of LINNAEUS.

Because of the varying radiation and heterogeneous composition of *Cosmarium* and *Staurostrum* there is rather large border-regions between these genera, the species of which are reckoned to *C.* or *St.* exclusively on basis of their bi- or triradiate structure, but which in shape not seldom agree more with species of the other genus. FRITSCH (1930, p 414 and 1933, p 34) has, in a detailed table, given an extensive comparison of several examples of these border-regions. Future investigations with finds of elucidating forms and subsequent distinguishing of new genera will diminish these border-regions. Within this area there is

in certain cases only a matter of chance or majority, whether the auctor has made the species a *Cosmarium* or a *Staurastrum*.

Previously a similar border-area existed between *Staurastrum* and *Arthrodesmus*. The latter genus was created already in 1828 as an improvement on the name *Scenedesmus* and contained originally *Arthrodesmus convergens* together with the straight two- or fourcelled coenobes of *Scenedesmus*. After the non-desmid character of the *Scenedesmus*-species had been recognized, the name *Arthrodesmus* was confined to the eight- or fourspined biradiate desmids with *Incus* as a prototype. Among *Staurastrum* there was a section with a smooth cellwall and one spine in each corner with the prototype *dejectum* which is quite in agreement with the incoid *Arthrodesmi*, except in the radiation.

The WESTS (Monogr. IV, p 99) changed the name of a form of *St. dejectum* to *A. triangularis* f. *triquetra*, it would appear for insufficient reasons, and commented: »It is in transitional forms of this kind that the distinction between the genera *A.* and *St.* breaks down». And, further, they (l.c. p 100) mention the occurrence of a triquetrous form of *St. triangularis* var. *subtriangularis* which possesses one semicell biradiate and the other triradiate. In their species *St. jaculiferum* they demonstrated it consisting of 2-, 3- and 4-radiate forms, and yet they were unable to perceive that the limit between adjacent parts of *A.* and *St.* was fallacious. At that time even these eminent desmid-experts were too prejudiced for the cleft between the monospinous biradiate *Arthrodesmi* and the similar pluriradiate *Staurastrum*. This border-area is now, as regards the monospinous species, eliminated, these are united into the genus *Stauroidesmus* (TEILING 1948). The few remaining species of *Arthrodesmus* still form a heterogeneous collection, some of them are nearly allied to species of *Staurastrum*, others to species of *Xanthidium*. The authors' opinion is that there is no justification for keeping even a reduced *Arthrodesmus* as a separate genus.

Another illustration of the paralysing effect of the *Staurastrum*-concept is NORDSTEDT's publication of *Staurastrum acarides* (1872, t 7: 26). He has delicate figures of it *a vertice* and *a fronte* and on the same plate figures of the very similar *Cosmarium tumidum* var. *triquetrum*. The latter was previously known as biradiate, i.e. a *Cosmarium*, the former was not!

There is a striking coincidence between the *Cosmaria* of *pseudamoenum*-type and *Staurastrum* of *pileolatum*-type: the (sub)cylindrical shape, the slightly constricted isthmus and the annular arrangement of the differentiated basal ornamentation. The staurastroid members of the

common type have their apices 3-, 4-, or 5-radiate with very short corners.

Another border-area of exactly the same kind contains the species of *Cosmarium capitulum*-type and *St. subpygmaeum*-type. These type-species are undoubtedly identical. The British form of *C. capitulum*, viz. var. *groenlandicum* is planktic and so is *St. subpygmaeum*, both in one case occurring in the same small lake. Algologist of recent time would have made a *C. capitulum* var. *triquetrum* instead of *St. subpygmaeum*.

Even between biradiate genera such border-regions exist, for instance *Euastrum* - *Micrasterias* and *Cosmarium* - *Euastrum* (FRITSCH 1933, p 22, *e.g.*). Intermediate forms are characteristic of Nature. Taxonomy involves our attempts to elucidate the obscurities in the relationships of allied forms. Desmidiologists, however, do not like rearrangement of their classical genera. Of course, many erected genera and sections have not proved sufficient or based on the right principles, this fact must not prevent us from new efforts. Desmidiology is not mere species-making, the species must be arranged into higher units, in well-founded genera!

*Euastridium* was established by the WESTS (1907, p 199, t 14: 11). In the diagnosis the authors call attention to *Euastrum* and to the most pronounced difference: »a vertice visae actinomorphicae, 8-lobatae». They make comparisons with the at that time only known triradiate *Euastrum*, viz. *humerosum*, and found the difference great enough to justify a separate genus. The original species is *E. Prainii* of which several specimens were found. The next species found is *E. staurastroides* N. CARTER (1926, p 287, t 1: 26) and the third also by N. CARTER *E. verrucosum* (1935, p 172, f 29, 30). At the same time PRESCOTT (1936, p 140, t 15: 11—15) published his find of *Staurastrum polonicum* var. *coronulatum*, identical with *E. verrucosum*. In an addendum PRESCOTT emphasizes the correctness of his placing it in *Staurastrum*. *Staurastrum polonicum* was established by RACIBORSKI (1884, p 17, t 1: 10) and excellently figured by DICK (1919, t 37: 3).

When these Desmids are examined from the point of view of their radiation, it appears that they belong to two somewhat different types. The one is characterized by corners provided with one tumour in the apical ring and two tumours in the basal ring, to this type belongs the triradiate *staurastroides* and the quadriradiate *Prainii* and *verrucosum*. The other type possesses corners, consisting of two tumours in the apical ring and three tumours in the basal ring: the bi- and triradiate



*polonicum*, f 30. The basal tumours may vary in number, RACIBORSKI's figure shows 6 apical and 8 (instead of 9) basal tumours but DICK's figure shows 6+9 tumours. DICK has another figure (1923, t 3: 9) showing 4+7 tumours, which must be regarded as a biradial facies.

There is no doubt that these four species belong to the same genus and this genus must be called *Euastridium*. In the collective genus *Staurastrum* there is a group, *Hoplastrum* TURNER, already dealt with, characterized by a similar structure, for instance *St. Tohopekaligense* with corners having 1+2 processes arranged as in the first above-named type, and *St. Arctiscon* with corners having 2+3 processes, as in *Eud. polonicum*. The granulate tumours of *Euastridium* and the terminally divided tubular processes of the *Hoplastrum*-forms are quite different things. The geometrical agreement, however, constitutes no reason for placing the four species in *Staurastrum*; the section of *Hoplastrum* being generically quite separate from the central group of the *Staurastrum*, built up on the original type, *St. paradoxum*. That this section has not yet been critically examined and delimited from *Staurastrum* is no argument against the maintenance of *Euastridium*.

According to this, *Euastridium* at present consists of:

*Sectio Trituberculatae.*

*E. staurastroides* N. CARTER, triradial, f 28.

*E. Prainii* W. et G. S. WEST, quadriradial, f 27.

*E. verrucosum* N. CARTER, quadriradial, f 29 (synonym: *Staurastrum polonicum* var. *coronulatum* PRESC.).

*Sectio Quinquetuberculatae.*

*E. polonicum* (RACIB.) n. comb., bi- and triradial, f 30. (non *St. polonicum* GRÖNBLAD 1938).

GRÖNBLAD (1931, p 2) once rejected *Euastridium* as a separate genus on the basis of its resemblance to *St. polonicum*. As argued above, this is no valid reason: RACIBORSKI placed the new species in *Staurastrum* having no other traditional genus to put it into. The only staurastroid element of *Euastridium* is the 3- and 4-radial structure.

GRÖNBLAD (1938, p 58, f 2: 8) has published an isolated find, one specimen only, of a desmid, named as *St. polonicum* which, however, seems to be identical with *Staurastrum insigne* LUND., a species holding quite a unique position within the *Staurastrum*, and almost worthy of the rank of a separate genus.

The weighty reason against an apprehension of *Euastridium* as a pluriradial section of *Euastrum* is the fact that no species of *Euastrum* possesses the double baso-lateral lobes. The forms, a fronte most similar

to *Euastridium* are, as judging from the literature available, *Euastrum verrucosum* var. *simplex* JOSH., var. *planctonicum* WEST, var. *subplanctonicum* GRÖNBL. and *Euastrum pingue*. *Eu. verrucosum* possesses, however, unpaired baso-lateral lobes and a prominent and beautifully ornamented frontal lobe. That this ornamentation is not to be seen in JOSHUA's drawing does not matter, for the WESTS found his drawings imperfect and sometimes »very much of a caricature». In triradiate forms of *Euastrum* the frontal ornament is preserved. *Euastrum pingue* var. *triquetrum* GRÖNBLAD (1942, t 1:35, fig. nostr. 26) is similar to *Euastridium staurastroides* but possesses simple baso-lateral lobes of cosmaroid character. *Euastridium* is a genus surely most closely allied to *Euastrum*.

The recently erected genus *Triplastrum* IYENGAR et RAMANATHAN (f 1—9) is in measure founded on deviating radiation.

### Vertical asymmetry among the desmids.

The symmetry of desmids is very seldom quite exact as some desmidiologists like to draw them, there are always small deviations in magnitude, proportions, ornamentation etc. Often the inequality of the semicells is striking. If not of teratological nature, these *dichotypical* (TEILING 1948) specimens often give hints on the relationship to other forms, species and even to genera. When the semicells exhibit different radiation, the dichotypical specimens are called Janus-forms (TEILING 1948). Such ones seem not to be uncommon in *Staurastrum* and *Staurodesmus*, from which the author has noted 33 cases in 25 species, most of them from his own research.

These species are: *Staurastrum alandicum*, *anatinum*, *Chaetoceras*, *cingulum*, *crenulatum* (NÄGELI 1849, t 8 B: k), *cyathodes*, *gracile*, *incisum*, *Kjellmanii*, n. sp., *paradoxum* (RALFS 1848, p 120), *pingue*, *planctonicum*, sp. (RALFS, p 120), *Staurodesmus aristiferus*, *cuspidatus*, *dejectus*, *jaculiferus*, *Joshuae*, *megacanthus*, *OMearii*, *sellatus*, *Spencerianus*, *subtriangularis* and *triangularis*.

In the following table the upper line signs the Janus-forms, (2+3) indicates one biradiate and one triradiate semicell together etc. The lower line signifies the number of cases, found in the actual form of Janus:

(2+3)	(2+4)	(3+4)	(3+5)	(3+6)	(4+5)
15	2	9	3	1	3

From this, although rather small, amount of material it seems as if the Janus-specimens with a difference of radiation more than one, are not so often formed as Janus of adjacent radiations.

Probably, dichotypical specimens are not uncommon. In the literature I have found only a few records. The earliest Janus-form is recorded by RALFS who devined its taxonomical importance. In many cases, however, desmidiologists do not record such specimens, regarding them as abnormal and of no interest, at least one scientist has told me this. On the contrary, they are of a very great interest and it would be very valuable if the specimens, met with, were described, carefully drawn and published.

The identity of *Staurastrum Thunmarkii* TEILING (1946, p 82) and *St. cingulum* is proved by means of Janus-forms. The author has (1948), in Janus-forms, given several examples of the identity or generical community of incoid *Arthrodesmi* and monospined *Staurastrum*. Dr. GRÖNBLAD has sent me figures of dichotypical specimens containing *St. Hantzschii* and *Tohopekaligense* and from Mr. A. M. SCOTT I have received a sample, containing cells, showing the characters of both *St. leptacanthum* and *Hantzschii* in one specimen. IRÉNÉE-MARIE (1939, t 58:9) has figured a dichotypical specimen of *St. Tohopekaligense* »servant de transition contre la variété *brevispinum* et la var. *nonanum*».

CUSHMAN (1908) says: »many of these so called varieties (of *Micrasterias*) are often seen forming one semicell of a specimen, the other semicell of which is typical, it seems hardly wise to recognize them as varieties». An intensive examination of the literature certainly would add many observations like this.

Attention must also be directed to the dichotypical form, presented by BOHLIN (1901, p 55, f 13) and showing the close relationship of *Staurastrum gracillimum* and *bibrachiatum*, an objection to the proposed genus *Dichotomum* WEST.

PLAYFAIR noted interesting »mixed forms» of *Staurastrum orbiculare* (1910, t 12: 19 and 1913, t 54: 26) in connection with advanced conclusions of its relations.

In *Cosmarium* and other genera with more concentrated semicells the dichotomy is preferably confined to the ornament and subsequently not so striking but easy to overlook. The examples of variation in *Spinocosmarium*, richly illustrated by SCOTT and PRESCOTT (1949) give proofs on dichotomy, which likely have prevented the authors from forming more varieties.

### Research on Radiation.

Only few desmidiologists have dealt with radiation as a concept. The WESTS have in several occasions touched upon the radiation when discussing the relationship of the desmids, certain species and in general. Their opinion seem to have been the following (G. S. WEST, 1904, p 144, W. and G. S. WEST, Monogr. I p 22). Omniradiate ancestral forms, represented by *Penieae*, have given rise to biradiate in the following series: *Tetmemorus* → *Euastrum* → *Cosmarium* → *Micrasterias*. They derive *Arthrodesmus* from both *Cosmarium* and *Micrasterias* via *Staurastrum* and *Xanthidium*, probably because of its spinous character. They consider *Arthrodesmus* as the starting-point of most of the filamentous genera. Only *Spondylosium*, *Phymatodocis* and *Hyalotheca* have arisen directly from *Cosmarium*. This phyletic series implies the following series of radiations: omniradiate → biradiate → pluriradiate → biradiate and from biradiate also a branch to omniradiate.

FRITSCH (1933) has accepted this hypothesis, at least the beginning of the series, and has tried to analyze the changes of radiation and its mechanism. He supposed that the median tumour of several *Cosmaria* may grow to a great enough extent to make the semicell quadriradiate, and based his opinion upon the great tumours of *Cosmarium Holmii*, which LOWE (1923, p 29, f 5) suggested should be placed in *Staurastrum*. This seems to be a rather weak basis; even the most extreme forms, figured by LOWE, are not to be interpreted in this way, and it is to be supposed that LOWE has not failed to publish his most prominent specimens. The same remonstrance must be made in relation to other *Cosmaria* with great tumours, BORGE (1925, t I: 8) has figured a form of *C. commissurale* var. *crassum* which is nearly a square *a vertice*.

FRITSCH supposed that the genesis of the triradiate type may have been performed in a similar manner, he mentioned *Cosmarium obliquum* with one plane and one convex front as a possible basis for evolution.

*Cosmarium obliquum* NORDST. was changed by RACIBORSKI (1889, p 48, t 8: 13) into a monotypical genus, which has not been accepted. Its shape *a vertice* is an ellipse with one side flattened, *a fronte* almost rectangular with a narrow, little isthmus. From the figures of diverse authores it appears that variation of considerable magnitude occurs. In f. *major* PRINTZ (1915, t 3: 55) and in var. *tatrica* GUTWINSKI (1909, t 7: 19) the vertical shape is distinctly semicircular, in var. *concauum* BECK-MANNAGETTA (1926, f 15) the straight side is incavated and in



KURZ' figure (1922, f 35) it is almost elliptical. W. WEST (1892, t 24: 15) described a f. *trigona*. This species certainly represents a rather unique form but it is, nevertheless, not more worthy of being regarded as a starting-point to triradiation than other biradiate desmids, sometimes appearing in triradiate shape.

PRESCOTT (1948) has accepted the idea of WEST and FRITSCH; he means (p 663) that the lot of triradiate *Cosmaria* supports the sequence: biradiate  $\rightarrow$  triradiate. From an other point of view, the inverse sequence is quite as logical. A wrong basis, common to most of desmidiologists, is discernible in PRESCOTT's further arguing on this subject, viz. the apprehension of *Cosmarium* and *Staurastrum* as genetical units, and, consequently, as prototypes for biradiate and pluriradiate desmids, possibly because of their richness in species. FRITSCH (1933) often has avoided this conception by speaking of »cosmarioid» and »staurastroid» desmids, quite as the present author has, in the same sense, used *Cosmaria* and *Staurastrum* or put the names into inverted commas.

HEIMANS (1942) has treated some finds of triradiate *Micrasterias truncata* and *M. Mahabuleshwariensis* var. *Wallichii*. Of the former species he found only one semicell triradiate, thus a Janus-form, though the triradiate semicells were not quite equilateral, one radius being stunted in growth. The latter species appeared in regular triradiate form, known also from other countries. Of interest are certain circumstances concerning the biotope and the distribution. The triradiate form was found regularly and constantly in several biotopes during ten years, in some of them exclusively the triradiate form, in one other together with the biradiate form. HEIMANS compares the genesis of the triradiate form with the peloric flowers of certain plants, but is well aware of the difference; in this case, the pleomeric changes occurring in a single protoplast under interaction of »organizing forces».

The intensive culture-research on the ontogenetic evolution of desmids by LEFÈVRE (1939) contains some contributions to the radiation-problem. Triradiate specimens of *Staurodesmus brevispina* developed in culture as well 4-radiate as also 5-radiate (f 103—113) specimens and *Cosmarium ochthodes*<sup>1</sup> and *C. impressulum* gave rise to a number of triradiate specimens. In pure-culture of single triradiate specimens of *C. ochthodes*, biradiate specimens appeared together with triradiate ones and in clones of 4-radiate *Staurodesmus brevispina* triradiate specimens appeared.

<sup>1</sup> According to DICK (1919, t 16: 5) *Staurastrum alpicolum* SCHMIDLE seems to be identic with *Cosmarium ochthodes* f. *triradiata*.

Natural clones of planktic *Staurodesmus triangularis* have been studied (TEILING 1948), containing 2-, 3-, and 4-radiate specimens as well as Janus-forms (2+3) f 24, (2+4), and (3+4) f 25. Very rarely young Janus-specimens, adhering after the division, have been observed. Of special interest was a case which consisted of one Janus (2+3) and one (3+4). Due to the adherence it could be stated that the mother-cell had been a Janus (2+4) of which the one semi-cell had increased the radiation from 2 to 3 in her daughter-cell, the other had decreased her daughter-cell from 4- to 3-radiate.

TURNER (1922) who had the opportunity to examine an extremely valuable material of *Staurodesmus Dickiei* in formation and also germination of zygospores, stated that in certain cases, of the four new daughter-cells of the germinating zygospore two were triradiate and two quadriradiate. And more, Janus (3+4) among triradiate cells of the primary tetrad were found.

The content of our present knowledge on the radiation seems to be able to be summarized as follows:

1. The radiation is unique to the desmids, no other unicellular Algae being symmetrical in three perpendicular planes, except the sphaerical Algae.

2. The variation is variable but in very different degrees, it increases in extent and frequency with rising numbers of radiation. The biradiation, characteristic of the majority of desmids, is the most constant radiation, *i.e.* its variation is in most cases latent. Biradiate desmids with multilobed edges (*Micrasterias* and *Euastrum*) or patterns of forked spines (*Xanthidium*) are more constant in radiation than desmids with solid body of the semi-cells and granulate or smooth cell-walls. Smooth and simple *Cosmaria* and *Staurastrum* often show a diffuse radiation or have developed into a false omniradiation. *Staurastrum* with short blunt corners are more pleoradiate, even in low radiation, than *Staurastrum* with long differentiated processes.

The causes of variation in radiation are unknown. In the first place it is supposed to be induced by ecological factors. The observations of LEFÈVRE, mentioned above, may perhaps be interpreted in this direction. A phytogeographical fact of somewhat similar kind is, that tri-radiate forms of well-founded biradiate desmids are found in subarctic and alpine biotopes, a feature stressed by Dr. R. GRÖNBLAD (*in litt*). A superficial examination of subarctic and alpine papers of NORDSTEDT, WILLE, GRÖNBLAD, N. CARTER, WHELDEN, and SCHRÖDER gave a list of 12 species of *Cosmarium*, 5 species of *Euastrum*, *Xanthidium anti-*

*Iopaeum*, *Staurastrum Natator* and *Bambusina Brebissonii* as triradiate, most of these not found elsewhere. On the contrary, TURNER's observation must be noted in the support of genotypical causes.

There seems to be a causal relationship between variability and formation of zygospores. Planktonic desmids exhibit a decided trend of variation both in radiation and in other respects. They form zygospores only in the most exceptional cases; indeed, they have very few opportunities. The author has never encountered any of them<sup>1</sup> and in the literature I have only noted *Staurodesmus triangularis* f. *rotundatus* (G. M. SMITH 1924, t 86: 4). The only place for zygospore-formation seems to be the litoral, the abyssal being too dark for desmids. Because of the rare possibilities of regeneration the planktonic desmids are forming immense clones during decades, maybe centuries. The mutations created are subjected to pure-culture during long time, and new forms, fitted to planktonic life, have been selected, giving rise to local races, not infrequently confined to one single lake (TEILING 1947). The often observed pleoradiation combined with Janus-forms in planktonic desmids may be a result of this degeneration; the trend of a fixed radiation lessens and also for other attributes.

### A theory of the mechanism and origin of desmid radiation.

In order to get a basic understanding of the radiation, an attempt to elucidate the probable cytoplasmatic mechanism seems justifiable. The starting-point is the genesis of a new semi-cell. This process has been carefully studied by LEFÈVRE (1939) in his cultures. On desmids with a constricted isthmus a separating wall is formed in the isthmus at the same time as the semi-cells are separating at their junction. Now each daughter-cell bulges out through the isthmus-hole, forming a vesicle enveloped in a «couche génératrice» formed by the above-mentioned separating-wall. By and by the vesicle is developed in shape and size. The cytoplasm produces the definite wall of the new semi-cell, whereupon the «couche génératrice» degenerates, is flaked off or becomes mucilaginous.

Already in the vesicle-stage the radiation is determined; the primarily subglobular vesicle grows out to become a semicell, elliptical,

<sup>1</sup> Dr. J. W. G. LUND, Wray Castle, has communicated (*in litt.*), that he, during five years' weekly examinations of plankton from Lake Windermere, has not yet seen a zygospore or conjugation. Windermere is very rich in desmids, both in quantity and number of species.

triangular, quadrate etc. *a vertice*. It is evident that the most peripheral layer of the cytoplasm is the form-giving agent, the »meristematic cytoplasm», the relative intensity of which is building up the micro-architecture of the semi-cell. In a semi-cell, circular *a vertice*, the meristematic cytoplasm is uniformly distributed in the periphery. The creation of anguloradiate semi-cells implies, that the out-growing in certain reciprocally aequidistant places is greater than in the intermediate parts. This presupposes a concentration of the meristematic cytoplasm into organelles in these places. In this connection the Janus-forms are illustrative. In certain species of *Staurastrum*, rarely forming Janus-specimens, there is a striking difference between the length of the processes of the semicells; the biradiate one having longer processes than the triradiate one. *St. cingulum* very seldom forms Janus-specimens, the processes of the biradiate form are stouter and longer than those of the triradiate one. The processes of *St. Chaetoceras* become about half the size on the triradiate semi-cell of the Janus-form (f 23). TEILING (1948) has noted this fact and has given figures of several examples in species of *Staurodesmus*. According to the line of thought mentioned the amount of meristematic cytoplasm, divided into three organelles, is not able to produce processes as long as in only two meristem-organelles.

The active duration and further differentiation of these cytoplasmatic meristem-organelles is very diverse, they may produce minute tumours, hardly discernible as small angles, *e.g.* *Staurastrum Merianii* (f 2—5), or they may produce long, narrow tubes, *e.g.* *Staurodesmus triangularis* (f 24—25), which afterwards are filled of wall-material to form solid spines, or they may produce elongated hollow branches, ending in small spines, *e.g.* the core of *Staurastrum*, or they may differentiate into more or less complex systems giving rise to the multi-brachiate corners of *St. Arctiscon* or to the extremely laciniate flanks of *Micrasterias Sol.* One or other of the meristem-organelles may stop its activity during the ontogenesis and give rise to so called intermediate forms (f 31).

In agreement with WEST and FRITSCH the author comprehends the ancestral forms of the desmids as having been omniradiate desmids with subsphaerical semicells. Within their diffuse parietal wall-building cytoplasm there has arisen a trend for concentrating or stimulating the action of growth in certain points round the »equator» of the semicells. Primarily many such meristematic organelles and subsequently corners or processes may have been the rule. The advantages of this



shape lie in the enlargement of the surface, favourable to the absorption of light and raw material and to the diffusion of oxygen in connection with the photosynthesis. The corners and also the processes (except the spines) contain branches of the chloroplast of the primitive central star-shaped type. Yet further it is, perhaps theoretically possible to get an approximate maximum of the radiation realized in simple processes like the primitive type *Staurostrum Victoriae* WEST, 11-radiate, f 32. The processes must have been wide enough to contain the branches of the chloroplast and it situated with very small interspaces, their number must not have much exceeded 12. With these must not be confused the creation of secondary processes, developed in desmids of lower radiation, for instance the *Hoplastrum*-section, previously mentioned. In these the primary meristem-organelles of the corners have been differentiated into groups of secondary meristem-organelles which have produced the processes. The formation of the secondary meristem-organelles may occur at once, e.g. *Staurostrum Arcticon*, or later, e.g. *St. furcigerum*, or by and by, e.g. *St. sexangulare* var. *supernumerarium*. All primarily hollow ornaments: *verrucae*, protuberances, spines etc., are due to secondary or tertiary meristem-organelles.

This primary whirl of processes has, in the course of evolution, been reduced in number, a reduction which has physiologically been compensated by the enlargement of the processes. This reduction has, in the most homogenous taxonomical units: *Micrasterias*, *Euastrum*, *Xanthidium* and other cosmarioid desmids, viz. certain sections of *Cosmarium* and the genera *Cosmocladium*, *Onychonema*, *Spondylosium*, and *Sphaeroszma*, definitively led to the end-stage, i.e. the biradiate desmids, compare the table on page 304 and f 34.

There is not the slightest reason to believe that Nature has, in this particular case, been directing the evolution in accordance with our arithmetical progression, beginning with 0 and, in this case, continuing with 2, 3, 4, 5 etc. as WEST in his hypothesis has taken for granted. On the contrary, there are so many important lines of evolution, both botanical and zoological ones, where the evolution has run its course from manifoldness to fewness. Here only some examples may be brought to mind. In the Arthropods the multiplicity of segments and legs of the older or more primitive forms, Crustaceans and Myriapodes, have undergone reduction to the two- or three-parted body and to the six- or eight legs of the insects and spiders. The seven gill-fissures of the more primitive Cyclostomes are gradually reduced in Selachians and Teleostei to three in the Batrachians. Perhaps the most striking, or, at

least the best known example is the reduction of the toes in the vertebrate-series; the primitively five toes being reduced to four, three, two and one! In the vegetable kingdom this trend of evolution is not so evident because of the simplicity of the organs, here may be remembered of the reduction of the microsporangia of the stamens, of the megaspores and, of all parts, petals, stamens and carpels of the floral shoots of the Angiospermes.

The trend of forming radiations of lower ranks is seen in Table I., the polyradiate species forming a very low percent of the total number. This is valid for the staurastroid desmids, but there is no reason to suppose these desmids having been, in their evolution, directed by laws, different to those affecting the biradiate *Micrasterias*, *Euastrum* and the *cosmarioids*. The biradiate genera must be considered as the most evolved, they have passed through the reductive evolution up to the end-stage and the cases of triradiation, found in them, are *atavisms*. As seen in the schema, p 323, the richness in radiations of the staurastroid desmids may be due to their being younger or retarded series of evolution. The study of Ecology shows that primitive characters may be successful in certain convenient combinations or under favourable ecological circumstances. The anguloradiate desmids, especially those with extended processes, gain more light than sphaerical ones. The general elongation of omni-radiate desmids is to be interpreted as another method for the enlargement of the surface; the elongation and the angular shape represent morphologically two quite different ways to a more effective photosynthesis. And furthermore, the pluriradiate desmids possesses one light-ecological advantage over the biradiate, especially over the most flattened; they are more independent of the direction of light. The leaf-like desmids are in an unfavourable situation, when turning the edge to light. This disadvantage may be compensated for by a more complex ability of phototaxis.

*In few words:* The angular structure has begun in shape of a whorl of processes from the subsphaerical semicell and proved successful to the photosynthesis. New mutations with fewer processes, near to hand, have arisen and among these the cells with lower radiation have proved more successful, because of the more effective exposition to light and a subsequent enlargement of the processes, as seen in the Janus-forms, have increased the favourable ratio *surface : volume*. The end-stage is the biradiate type, which exhibits the ideal form of the organs, executing the photosynthesis, *viz.* the *phyllloid* type, in the desmids for ever realized in *Micrasterias*, the thallus of higher Algae, Lichens and

Hepaticae and the leaves, phylloids, and cladophylls of Archaeogoniates and Phanerogames.

The transition from higher to lower radiations may have been performed through Janus-forms. This coincides with several facts, mentioned above. At first, the radiation is more fixed in biradiate desmids than in pluriradiate ones and among these the triradiate desmids are less pleoradiate than the polyradiate ones. Janus-forms are very rare in biradiate desmids, but so common among the polyradiate that many desmidiologists find this fact not worthy of mentioning.

Sometimes there are found specimens with stunted supernumerary radial processes, they have been interpreted as a beginning of a higher radiation, according to the hypothesis of WEST. On the contrary, stunted processes are rudiments of a higher radiation. In the juvenil semi-cell there have been more meristematic organelles than specific ones, during the ontogenetic development the supernumery meristematic organelles have been stunted in their growth; they are typical rudiments. Fig. 31 shows a semi-cell of *Staurastrum anatinum*, preliminary 6-radiate, two processes have been stunted, at first the one and somewhat later the other. After this the semi-cell has developed as a 4-radiate one, which is proved in the four rows of marginal verrucae, formed later on.

Fig. 34 is meant to make clear the author's view of the relation between the diverse radiations. Omniradiation is the primitive, still existing in several genera. From omniradiate ancestors polyradiate types have emanated and, under the influence of a reducing trend, lower ranks of radiation were created. The »royal road» from omniradiate to biradiate and other radiations of lower rank passes, ontogenetically, through the possibilities of, phylogenetically, higher radiations and, under the influence of unknown causes, the development of the semi-cell may take a wrong turning into a radiation, not agreeing with the normal or even with the radiation of the mother-semi-cell. This reasoning explains the frequent variation of the radiations among the polyradiate *Staurastrum*; the nearer the meristematic organelles have been differentiated in the primarily diffuse meristematic cytoplasm, the greater probability of an alteration in number.

The biradiate desmids are stated to be very constant in their radiation, especially the most flattened and ornate. Certain *Cosmaria* and *Staurastrum*, having homogeneous semi-cells with short angles and smooth or granulated cell-wall, show a shape *a vertice* of a very broad ellipse or a rather circular triangle, e.g. *Cosmarium tinctum*, *C. aversum*,

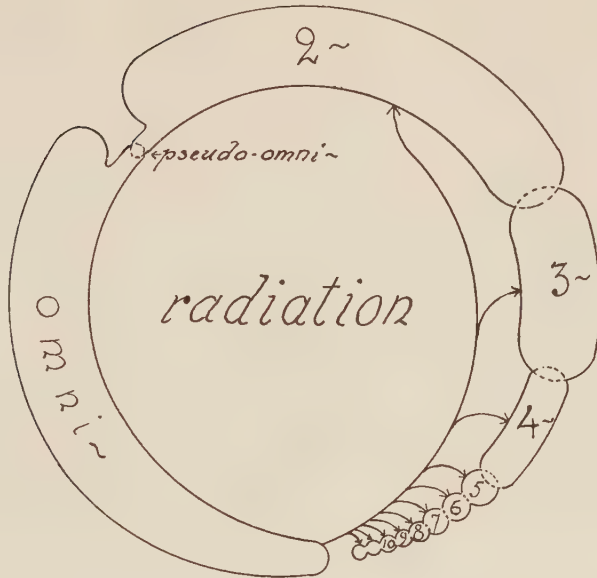


Fig. 33. Diagram, showing the development of radiation. The *phylogenetical* line leads from the omniradiate area over the circles, indicating radiations from 12-, up to 2-radiate forms. The increasing surface of the radiation-areas will indicate the increasing number of forms. The branched line from the omniradiate area indicates the *ontogenetical* development.

*Staurostrum orbiculare*, *St. Merianii* (f 1—5), *St. inflatum* (f 10) and leads over to pseudo-omniradiation. This indicates a minimal activity of the meristematic organelles. The *Staurostra* mentioned belong to a group with blunt corners where the radiation is the most variable among the «normally» triradiate *Staurostra*.

In *Cosmarium* this has led to a false omniradiation, *C. moniliforme* e.g. An instructive example is *C. excavatum*. This species is in the diagnose «a vertice visum orbicular». WILLE has figured a sub-circular var. *ellipticum*, STRÖM a broad-elliptical var. *horizontale* and LAGERHEIM has described var. *trigonum*, a vertice triangular with somewhat inflated flanks, also found by WOLLE. It seems difficult to imagine a genuine omniradiate semi-cell being also bi- or triradiate. The true nature of it is, most probably, a slightly pronounced biradiation, sometimes transferred into triradiation but in most cases diffuse enough to form a circular shape, *pseudo-omniradiation*. From their point of view the WESTS regarded the var. *trigonum* as «very possibly a species» of *Staurostrum* (Monogr. III, p 147). According to the theory submitted,



this transition between omniradiation and biradiation, but in the inverse direction, is the only right idea of G. S. WEST's interpretation. Among clearly omniradiate desmids some cells may be slightly elliptic in end-view, this is, however, no biradiation, only a compression of a cylindrical cell due to edaphic causes.

The theory of the evolution of radiation submitted is intimately bound up with the structure of the chloroplast. The star-like axial chloroplast with radiate plates is to be regarded as the »primitive one in desmids as a whole» (WEST 1916, p 365), confirmed by N. CARTER (1919), and this type can be followed in all radiations. In primitive omniradiate and pluriradiate desmids, the radiate chloroplast is typical, in thick biradiate desmids, *Cosmarium* and *Euastrum* e.g., the radiate structure is quite evident, also when the chloroplast is divided into several parts, and even in the most flattened species of *Micrasterias* (N. CARTER 1919) the fragments of the radial plates are still discernible. Primarily, the *radii* are bulges caused by and built around the extending branches of the star-like chloroplast in its trend to increase the light-absorbing substance.

This conclusion is not depreciated by the fact that some species have parietal chloroplasts, which signify an advanced adaptation to light-ecology. The parietal types of the chloroplasts are proved to be derived from the axial one, according to the investigations of LÜTKE-MÜLLER and N. CARTER. Parietal chloroplasts occur only in omniradiate, broad-elliptical biradiate or short-angular triradiate desmids. There are certain common features of these desmids, viz. a large surface without tumours, realized in an elongated body in omniradiate types, *Pleurotaenium* e.g., and a large body of the bi- and triradiate desmids, all of them among the biggest desmids on the whole, for instance *Xanthidium*, *Cosmarium*, *Cucumis*, *C. Ralfsii*, *C. ovale*, *Staurastrum tumidum*, *St. grande* and *St. longispinum*. The most flattened *Micrasterias* have solved the problem in a perfect manner: their chloroplast being lateral in function and axial in origin.

### Phylogeny of Desmids.

Finally the author wishes to submit some indications of the influence, which these new points of view on radiation may have upon our apprehension of the phylogeny of desmids. In fig. 34 the author's present opinion of the phylogenetical relations of certain genera of the

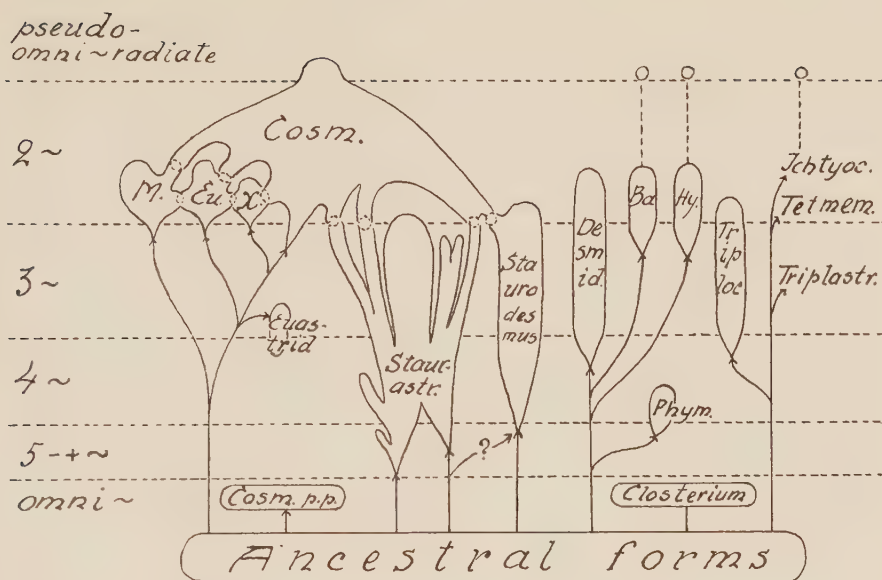


Fig. 34. Phylogeny and radiation of certain desmid genera.

*Placodermeae*, essentially based on the radiation, is exposed graphically, not considering other principles presented by FRITSCH (1920, p 404).

The schema, giving the genera a more differentiated origin from omniradiate ancestors, differs fundamentally from the schema of origin, presented by G. S. WEST (Monogr. I, p 22) where he makes the genera forked-points instead of branch-ends. The internal relations within the bulk of «ancestral forms» are not touched upon, a test being at present impossible. According to the author's opinion about the importance of radiation as an evolutionary principle, the phylogenetic tree is arranged on a background of the stages of radiation, on which also the pseudo-omniradiation is paid attention to. The abbreviations of the names may be easily understood.

The «amöboid» shape of the *Cosmarium*-area is to be interpreted in such manner that *Cosmarium* is the common name of several different biradiate groups. The central group is not sharply delimited, having marginal-areas common to several genera: the relatively uniform *Micrasterias*, *Euastrum* and *Xanthidium* and also to differentiated parts of the collective genus *Staurastrum*. The cosmarioid branches of these genera possess characters which are covered by the extremely diffuse diagnosis of the «genus» *Cosmarium*. Strictly speaking, there is no

definite, positive character applicable to *Cosmarium*. The WESTS, who in 1905 represented the most extensive knowledge of the species of desmids, were, in their Monograph II, p 126, unable to fix the limit more sharply than: the *entire* outline and the lack of spines. Now, 45 years later, even this delimitation is not applicable.

The marginal-area to *Staurodesmus* will reinforce this, for because of the reduction of spines, there are species of *Staurodesmus* producing *formae inermes* which are reckoned to *Cosmarium*, e.g. *Std. convergens*, *Std. brevispina*. The lobe, overlapping the limit of the pseudo-omniradiate area, signifies the group of *Cosmarium moniliforme*, previously mentioned. Another group of *Cosmarium*, containing the omniradiate *Penium*-like species, is placed quite apart of the main-part.

Also *Staurostrum* is indicated to be polyphyletic. This fact, already pointed out by FRITSCH (1933), is confirmed by the occurrence of the different types of zygospores in these genera, as seen from the valuable tables of FRITSCH.

*Bambusina*, *Hyalotheca* and *Ichtyocercus* are marked as nearly pseudo-radiate.

### The Radiation and the Nomenclature.

In the preceeding exposition the author has emphasized that the radiation of desmids is a fundamental feature of their structure, not to be found in other groups of organisms. It has been used in distinguishing *formae*, *varietates*, *species* and even *genera*. It signifies a leading line of their phylogeny.

Nevertheless, this radiate point of view has been disregarded and when distinguishing specimens of a species, appearing in diverse radiations, there are neither terms nor rules of nomenclature. Some authors have used the variety-name, other the forma-name and an author may use the one or the other name depending on conveniency, see p 302. Both are, however, irrelevant. The concepts of *varietas* and *forma* are used in Desmidiology in order to signify deviations from the, often accidentally, created concept of a species. The only difference discernible in the capriciousness of their use is, that *varietas* is intended to indicate more important differences of shape or ornamentation, and the *forma*-name is usually followed by *major*, *glabra*, *extensa*, *crassa* etc. A general tradition is that the first deviation described is regarded as a variety of whatever kind it may be, and a later found deviation of this variety is indicated by *forma*, a concept of lower rank or found later on.

Actually, the radiation is not to be compared with the features usually »commemorated» as varieties and *formae*. An attempt to use the term *subspecies* (TEILING 1948) can not conveniently be continued, this concept being preferably used on chorological units and thus not applicable to the actual purpose. In default of an adequate nomenclatorial term a term *sui generis* must be created.

The present concepts and especially nomenclatorial terms of desmid taxonomy date from RALFS' time, only a century ago but yet from the childhood of Desmidiology. Since then an immense material has been collected and described but quite in the manner of RALFS' time. Only during the last decades, under influence of improved methodes a more fundamental research is developing. The wider points of view, given by Evolutionism and general Biology have not been acting as stimulus to Desmidiology, owing to the desmidiologists, most of them too prejudiced. Thus, the development of modern Biology has not been able to penetrate and stimulate desmid-research because of the lack of the necessary concepts and corresponding nomenclatorial terms.

In a memorial, sent to the Commission for Nomenclature of Algae and intended to be dealt with at the Botanical Congress this year, the author has developed these points of view and proposed the term *facies*, abbreviated *fac.*, intended to be used in nomenclatorial expressions indicating the radiation. For instance: *Micrasterias Murrayi fac. triquetra* WEST, *Euastrum pectinatum var. brachylobum fac. triquetrum* KAISER, *Xanthidium armatum fac. triquetrum* ALLORGE, *Cosmarium excavatum fac. trigonum* LAGERH., *Staurastrum cingulum fac. Thunmarkii* TEIL., *Staurodesmus cuspidatus fac. tricuspidatus* (BRÉB.) TEIL., *Staurodesmus OMearii fac. Wandae* (RACIB.) TEIL., *Desmidium Swartzii fac. quadrangulatum* (RALFS) ROY, *Staurastrum Ophiura fac. 9-radiatum*, *Hyalotheca dissiliens fac. tridentula*. A further advantage is the circumstance that the *facies*-indication, being independent of the varieties and *formae*, can be placed before or after the indications of *varietas* or *forma*.

In the proposal also the use of the term Janus is proposed. The use of Janus (TEILING 1948) contains a statement of the radiations, combined in figures, for instance *Staurodesmus triangulum* Janus (2+4), *Staurastrum Chaetoceras* Janus (2+3), *St. Ophiura* Janus (6+7). By contrast with the manner of use in TEILING (1948) the Janus-indication is to be used without preceeding f. and exclusively to specimens with different radiation. In dichotypical specimens, showing a com-



bination of different species, varieties or *formae*, the Janus-expression must *not* be used, *St. furcigerum*+*f. eustephana* e.g.

The term *facies* (face) alludes to the fact that a genetic species may show different faces to the observer-scientist, like an actor changing his masks to mystify or elucidate him. The term Janus is quite in concordance to *facies*, the name of the double-faced god of classical Antiquity.

The author's motive has been to bring about terms, intimately corresponding to the concepts, new or more definitively cleared up, to which the old comprehensions of varieties and *formae* are not homologous. A further motive is that a separate term lays emphasis on points of view, well worthy of study, and that the results of these studies will prove fruitful for the future development of Desmidiology and Science.

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## The conservation of species names.

The question of *nomina specifica conservanda* will be taken up at the International Botanical Congress this year. As this is a question of great practical consequences for all botanists, the editor has asked some prominent botanists, who could be expected to be especially interested in the matter, for their views on the subject. The following answers have been received.

### Dr. H. W. Rickett (New York Botanical Garden):

In approaching the problem of the adoption of *nomina specifica conservanda* there are, it seems to me, two principal questions to be answered: Will it work? Is it necessary? If there is a reasonable doubt about either question having a positive answer, then the conservation of specific names must fail.

Will the establishment of a list of binomial exceptions to the rules of nomenclature effectively solve the problems which it is designed to solve? Will it increase the convenience of binomials to those who must use them? Will it make for stability in nomenclature?

There are those who think that *all* names should be fixed by law. This point of view is held by those who are ignorant of the workings of taxonomy and the possibility of increase in our knowledge of plant relationships. Taxonomists know that changes in names often result from changes in classification; they are necessary concomitants of advances in knowledge. Any legislation, therefore, can conserve a name only in its present sense and usage — it cannot close the door to future change. If a species is transferred to another genus, or moved to a new rank, or if taxa of other categories undergo such changes, their names *must* be changed accordingly. In this respect generic and infrageneric names differ. No list of *nomina specifica conservanda* can have the stability of *nomina generica conservanda*. Even if only the epithets are conserved (which would be possible), the user might still have to

accustom himself to using them with another genus or in another position.

Some clue also to the possible working of such a list may be gained from scrutiny of the current condition of conserved genera. Many who once advocated the establishment of *nomina generica conservanda* must now regret it. What was meant to be the means of stabilizing a few well known names has become a juggernaut grinding its way over the principle of priority. An elaborate index is already necessary to determine the status of a generic name; it is possible to contemplate a future in which the exceptions to the rules may outnumber the names which conform! Where would twenty years of conservation of specific names take us?

Second, is conservation necessary? Those who must use names and are not nomenclators — not only taxonomists but physiologists, geneticists, foresters, teachers, and so on — have, at first sight, a very good cause for fixing specific names in common use. It is certainly disquieting to abandon a name which is found in dozens of textbooks, seed catalogues, popular books, as well as works on forestry, ecology, pathology, genetics, and so on; and to substitute a name which no one has ever previously used. The flaw in the argument is that »science is long and life is fleeting». What seems a nuisance in the life of one man is trivial in the history of science. The same sort of argument has been used to preserve the old names of eight families as exceptions to the rule for naming families: *Palmae*, *Gramineae*, *Cruciferae*, etc. But what has become of such names as *Exogenae* and *Endogenae*, *Phanerogamae* and *Cryptogamae* and *Amentiferae* and *Acotyledones*? To abandon any of these must have seemed to the botanists who were using them the end of all stability in nomenclature; and some of them were in very common use. Now such names as *Thallophyta*, *Pteridophyta*, and *Archichlamydeae* are on the way out, with the usual reluctance on the part of teachers and others.

Again some idea of the necessity for conserving specific names may be gained from a look at generic names. After a short initial period of unfamiliarity, the prior names of practically all genera would by now be in everyday use, and the new generation of botanists would not be disturbed by them. (Many rejected names were once familiar to many botanists.) Our struggles with specific names, likewise, will not continue indefinitely — except as they are made necessary by advances in knowledge.



**Professor K. Gram (Copenhagen): Are nomina specifica conservanda wanted?**

The article 21 in *The International Rules of Botanical Nomenclature*, 3rd edit. 1935 and the additional notes together with the supplementary article 22 concerning conservation of certain generic names have proved to be extremely valuable. It is the opinion of the present author, that the want of similar rules for the specific epithets is one of the main drawbacks in the applicability of the rules in force. Furthermore the author has become convinced, in discussing nomenclatural problems with other botanists and with practical scientists from horticulture, agronomy and forestry, that the demand for fixed names of the species, as far as possible, is widely spread and justified by the amount of recent alterations and realterations of specific names due to the existing rules; besides, in many cases it seems to be almost impossible to come to any agreement on the valid epithet of certain species.

As a contribution to the discussion on the justification of introducing a new article on the conservation of specific names in the Rules, the following items may be mentioned.

1. Fixed names must be considered to be a necessity for the use of scientific results if not lots of time are to be wasted. The more *Nomina Specifica Conservanda* may be established, the better scientists will be able to work and their results be available in practice. The author thus fully agrees to the justice of the claim of fixation of the names of plants. A new article on the conservation of specific names ought to be proposed at The Seventh International Botanical Congress as a highly wanted amelioration of the existing rules of nomenclature. As in the case of *nomina generica conservanda*, lists of such epithets must be published by a committee of nomenclature as proposals to be enacted at a new international congress. The highly appreciated nomenclatural work hitherto made by so many taxonomists naturally may be utilized by the committee, which too, must take into consideration the following items amongst several others.

The most effective plan which, however, unfortunately seems to be Utopian, would be to establish a list (*Index Specierum Plantarum*) containing fixed names of all known plants and of their described varieties with references to the original descriptions. Besides all synonyms, this index ought to bring legitimate (fixed) combinations in cases of transference of a species to an other genus or alteration in taxonomic rank.

2. Names, that, ever since they were published in connection with the first valid description, have been commonly used by all or most botanists, ought not to be rejected on account of little known or even unknown names that may be found in obscure papers and local floristic literature.

Example: *Abies nobilis* LINDL. 1833 non DIETRICH 1824 (up to 1940 the only epithet of this species) must be preferred to *A. procera* REHD. 1940, although the latter is given by REHDER in accordance with the Rules and in consequence of the earlier homonym wrongly used by DIETRICH as a name of *Abies alba* MILL. 1768.

3. Due to the Rules the name of Austrian Pine is very uncertain. *Pinus nigra* ARN. 1785, which has been used for years, has recently been rejected because it may be interpreted as a nomen provisorium or nudum (or at least subnudum). *P. nigricans* HOST 1826, has then been considered to be the first legitimate name if *P. nigra* has to be deleted, but now we know that the western variety of this species was called *P. Clusiana* before any other valid name was published except the dubious *P. nigra*. Many other names have been commonly used for this tree, e.g. *P. austriaca* Höss and *P. Laricio* LOUD. In this and similar cases the fixation of one of these names as a nomen conservandum is highly requested, and if asked, the author would propose *P. nigra* ARN. (cfr. the last passage of point 4).

4. In the cases of nomina dubia and nomina ambigua it very often happens that botanists cannot come to agreement either on what is doubtful or on the sincerity of the confusion; hence, such plants are dealt with under two (sometimes even more) epithets. This has to be avoided.

Example: In American literature the Balsam Poplar is often called *Populus Tacamahaca* MILL. while most European botanists prefer to call it *P. balsamifera* L. One of these names must be fixed; on account of statements by HOUTZAGER and HYLANDER the author is of the opinion that there is no compelling necessity to reject the name given by LINNÉ, and that this name ought to be fixed in order to avoid further discussion. But if a majority of botanists would prefer MILLER's name, the author will agree to it, because it is of much more importance to have fixed names of the taxonomic units than to find names of an earlier date and to discuss for ages the validity of two or more names of the same species.

I believe that all botanists of the coming ages will be extremely grateful, if we, the sooner the better, start this work on stabilization of plant names on the basis of as many *Nomina Specifica Conservanda* as possible.

**W. H. Camp (Philadelphia, Chairman, Committee on Nomenclature,  
The American Society of Plant Taxonomists):**

The International Rules of Botanical Nomenclature clearly state (Art. 4) that the primary point of the Rules is »to aim at fixity of names». Taxonomists therefore should welcome any addition to or modification of the Rules which really will implement this ideal.

Starting with the basic concept of priority as a method of stabilizing nomenclatural practices (in the spirit of the present Art. 16), it soon became apparent that absolute priority would introduce chaos. Therefore a statute of limitations was introduced. The result was the apparently modifiable and elastic Art. 20, having to do with »starting dates». Here was another equally brave attempt to stabilize nomenclature. However, this also left something to be desired and so Art. 21 was formulated, exempting the names of genera from strict priority and effective starting dates. All this was done in an honest attempt to arrive at fixity of names.

There certainly is no equivocation in Art. 27, for it clearly states that »Names of species are binary combinations consisting of the name of the genus followed by a single specific epithet.» If the name of a species is to be thus designated it therefore follows that the name of an individual of the species also will be the same binary combination. One can but wonder why, when special rules were formulated to stabilize the names of plants, only the generic name was taken care of, with the specific epithet left out in the bleak world of arbitrarily chosen starting dates and strict priority. It would seem only consistent — if we are to have *nomina generica conservanda*, and if there be any consistency in nomenclature — that some method should have been devised, long before this, whereby we might have achieved our stated ultimate goal of nomenclatural stability through an additional provision for *nomina specifica conservanda*. One therefore is still curious, with Art. 21 a *de facto* nullification of Arts. 16 and 20 (the basic principle of priority and of effective starting dates), why it was not extended to the specific epithet. Can it be that the delegates to former Congresses, who firmly rejected each attempt to introduce *nomina specifica conservanda*, were less aware of the desirability for stability of specific

names than those who now advocate the measure? Or is it possible that they more fully understood the consequences of such action?

The conserved generic name is a *fait accompli*. Any attempt at this time to return to the principle of priority and fixed starting dates for generic names would only add chaos to the confusion. However, before we attempt complete consistency by adopting conserved specific names it might be well to consider several items.

The present compiled list of conserved generic names occupies 61 pages of text, and this in small type and a format designed especially to conserve space (1). The index to this list, now almost a necessity because of its size, runs for another 18 pages. The number of conserved generic names in Section X — Phanerogamae (Siphonogamae) — now approaches 800, with many more likely to be added in the near future if even a reasonable proportion of those currently proposed for conservation are provisionally approved by the Executive Committee (see Art. 22). I do not decry this activity; I only wonder how long it will continue and to what proportions this list will yet grow.

The proponents of *nomina specifica conservanda* usually assure us that the list will not be a long one — that perhaps less than a hundred specific names will be involved, and these in important horticultural, arboricultural, and similar groups containing economic plant materials. Yet in spite of these pious protestations I honestly cannot see how the list is to be limited by any adequate or impartial means. If we are to conserve the name of some crop plant then, to be consistent, we also should conserve the name of the weed which competes with it for space in our fields since, thus, it enters the sphere of agro-economy. It would be equally consistent to admit to conservation the name of a species which does not become weedy; it therefore may be planted near crop-lands for erosion control, or as shelter or food for game birds and small animals, thereby also entering the realm of agro-economy. Stripped of all sentimentality it becomes immediately obvious that foresters, horticulturists, and similar workers cannot lay claim to a prior need for *nomina specifica conservanda*. The needs of plant geographers, ecologists, and those working in other fields perhaps outside the immediate sphere of economic plant materials must also be considered, for they have equal rights. Any attempt to be impartial will require that the bars be thrown completely down.

One therefore wonders just how large the list of *nomina specifica conservanda* might ultimately become. In the beginning, the proponents of conserved generic names also assured us that the list would not be



large. Are we again being lulled by the same dulcet words from those who propose that we should conserve specific names? An admittedly hasty check of various geographic areas and plant groups indicates the possibility that a basic, *minimum* list of specific epithets which »ought to be conserved» might be in the neighbourhood of 2,500 names for the seed-plants only. If our experience with the conservation of generic names is any indication, this list of specific names might ultimately be further swelled almost to fantastic proportions. And I have yet to peruse any proposal which clearly indicated either a complete understanding of the ramifications of the situation or a practical method for keeping such a list within reasonable bounds.

Our experience with conserved generic names already indicates that certain decisions were too hastily made. It is to be understood that I do not criticize former Executive Committees in this statement. It is almost mechanically impossible for such a Committee to examine fully each case coming before it, beyond a consideration of the arguments set forth by the proposer. The proposer, usually acting in good faith and with the very best of intentions, may not have been in possession of all the pertinent literature. It is obvious that the supposed safeguard implied in Art. 22 has not functioned as was intended. Many such proposals are made by individuals who desire to use the names in their writings. Therefore by the time the next Congress convenes the proposed name, instead of having merely been examined and tested by taxonomists in the interim, already is firmly imbedded in the literature as a *de facto* conserved name. Any attempt to rescind the former approval of the Executive Committee would, by that time, only bring additional confusion.

Thus far the proponents of the conservation of specific names have not been completely clear how it is to be mechanically handled. Some have advocated that special groups appoint committees to make up lists of »accepted» names. Does this mean that the foresters, the horticulturists, the Rhododendron enthusiasts, the members of the Begonia Society, the ecologists, groups of European botanists, American botanists, the botanists of South Africa, minor geographical groups, or groups representing special interests or disciplines, will be at liberty to appoint committees and draw up independent lists of names which they will and will not use? The fact that several committees exist, or are in the process of formation, whose avowed purpose is to do just this — and completely independent of each other and outside any association with the Executive Committee — indicates the gravity of

the situation. Sanction of such uncoordinated and sometimes irresponsible activities would soon plunge plant taxonomy back into the same condition it found itself nearly a century ago when DE CANDOLLE was commissioned to draw up a series of »Laws» designed to extricate it from the slough of nomenclatural confusion. And certain proposals, leaving the decision as to which specific name is to be conserved to the judgment of the individual proposer, could lead only to utter chaos for, then, whims and personal prejudices would be the deciding factors.

In setting down the foregoing I have not said that *nomina specifica conservanda* would necessarily be a bad thing for plant taxonomy. I am not a botanical bibliophile — an archaeologist of the literature — and one of those who feel that a prior name is necessarily the »correct» one. I am in essential agreement with those who point out the advantages to be gained through the retention of familiar names sanctioned by long usage. Nor would mere size seem to be a valid deterrent to the preparation and critical editing of such a list. However, before an International Botanical Congress moves to open the flood gates to the possible effects of any such proposal it should carefully consider ways and means either of controlling the size of the list or of handling the situation should the seemingly inevitable result of uncontrolled conservation descend upon us.

At the present time the Executive Committee and Editors of the Rules and lists of conserved names contribute their own time (or that of their respective institutions) to this onerous labor. Should the list of proposed specific names swell to its possible proportions — and I see no really impartial or practical way of limiting it — a professional, full-time, paid staff of considerable size might well be needed merely to take care of the necessary multilingual correspondence and critical editorial work. At present no international organization with such a staff exists. Therefore, I consider it most unrealistic and impractical even to consider the proposition until we have such an organization.

It should be noted here that a group of 55 members of the American Society of Plant Taxonomists (together with associated groups) recently considered a proposal having to do with the conservation of specific names; it was rejected by the overwhelming vote of 53 to 2. This representative group of active, professional taxonomists, whose individual names are on record elsewhere (2), apparently was quite aware of the many possible pitfalls which await taxonomists should they once sanction this line of action.

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**Professor Erwin Janchen (Wien): Die Zweckmässigkeit einer  
Ausnahmsliste für die Namen der Pflanzen-Arten.**

Die Pflanzenwelt hat für das Leben und die Wirtschaft des Menschen in verschiedenster Hinsicht eine überragende Bedeutung. Die Pflanzenkunde, die Botanik, ist daher eine Wissenschaft, die nicht nur einen beschränkten Kreis von Fachleuten und Liebhabern angeht, sondern darüber hinaus auch die Gärtner, Landwirte, Forstwirte, Apotheker, Ärzte, Tierärzte, Techniker usw., überhaupt alle Menschen, die irgendwie mit Pflanzen zu tun haben. Botanik ist also eine äusserst lebensnahe Wissenschaft. Daher muss sie auch eine Sprache sprechen, die sich leicht verstehen und leicht erlernen lässt. Darauf die gebührende Rücksicht zu nehmen, sind die Botaniker ihren Mitmenschen gegenüber verpflichtet. Dies muss man sich auch bei allen Belangen der wissenschaftlichen Namengebung, der Nomenklatur, stets vor Augen halten.

Artikel 3 der Internationalen Regeln für die botanische Nomenklatur besagt: »Die Nomenklaturregeln sollen einfach sein und müssen auf so klaren und überzeugenden Gesichtspunkten beruhen, dass jedermann sie begreift und geneigt ist, sie anzunehmen«. Diesem leitenden Gesichtspunkt entspricht die Nomenklatur nur dann, wenn sie vernünftig ist, wenn sie nicht Namen bindend vorschreibt, die unvernünftig und sinnwidrig sind. Denn gerade Menschen mit einem unverdorbenen Gefühl für Sinn und Vernunft werden niemals geneigt sein, derartige Namen anzunehmen und sie werden die Notwendigkeit solcher Namen niemals begreifen. Manches in den gegenwärtigen Regeln steht in scharfem Gegensatz zum Geiste des Art. 3.

Artikel 4, Punkt 1 besagt: »Es ist Beständigkeit in den Namen anzustreben.« Aber gerade die strenge Befolgung der Regeln ist eine Quelle fortgesetzter Unbeständigkeit und Unsicherheit.

Die Grundlage der jetzt geltenden Regeln wurde im Jahre 1905 in Wien beschlossen. Ich habe damals alle Nomenklaturberatungen mit lebhaftem Interesse verfolgt und auf die Beschlüsse grosse Hoffnungen

gesetzt. Die Erfahrungen der seither verflossenen 45 Jahre haben gezeigt, dass trotz mehrfacher Änderungen der Regeln, die leider nicht durchwegs Verbesserungen waren, der Erfolg der Regeln nicht restlos zufriedenstellend war. Vor allem hat sich erwiesen, dass es nur durch Regeln allein, die man mit folgerichtiger Unentwegtheit ausnahmslos durchführt, überhaupt unmöglich ist, zu einer dauerhaften und beständigen, gleichzeitig mit dem bisherigen Gebrauch möglichst übereinstimmenden Namengebung zu gelangen.

Immer deutlicher konnte man erkennen, dass zur Erreichung einer dauerhaften und zufriedenstellenden Nomenklatur ausser einer Ausnahmsliste der Gattungen, die ständig ergänzt wird, auch eine *Ausnahmsliste der Arten* unerlässlich ist. Ich habe den Eindruck, dass die Zahl jener Botaniker, welche zu dieser Erkenntnis gelangt sind, ständig zugenommen hat.

Die Ausarbeitung einer solchen Ausnahmsliste wird gewiss eine sehr mühevollen Arbeit sein. Aber der Erfolg einer wirklich guten Ausnahmsliste wird sicher diese Mühe lohnen. An der Ausarbeitung der Liste müssen Fachleute für alle geographischen Gebiete (Länder oder grössere Einheiten) beteiligt sein und es müssen die Wünsche der Vertreter aller Zweige der angewandten Botanik, insbesondere der Gärtner, Landwirte, Forstwirte und sonstigen Nutzpflanzen-Fachleute gebührende Berücksichtigung finden. Gerade dieses letztere halte ich im Sinne der eingangs geäusserten Gedanken für sehr wichtig. Selbstverständlich wird die Ausnahmsliste nach ihrer erstmaligen Fertigstellung späterhin fortlaufend ergänzt werden müssen. Es wird unvermeidlich sein, dass die Liste einen ansehnlichen Umfang annimmt. Eine kurze Liste würde ihren Zweck nicht erfüllen.

Welche Gruppen von Pflanzen sind in der Ausnahmsliste der Arten zu berücksichtigen?

1. Nutzpflanzen und sonstige praktisch wichtige Pflanzen, also auch Zierpflanzen, Giftpflanzen, Unkräuter usw.;
2. sehr häufige, sehr auffällige oder aus anderen Gründen sehr bekannte Pflanzen;
3. Pflanzen, die geobotanisch oder pflanzensoziologisch wichtig sind;
4. Pflanzen, deren Namen sich durch bekannte gute Monographien stark eingebürgert haben;
5. erst in letzter Linie auch sonstige Pflanzen.

Nach welchen Gesichtspunkten sind durch die Artenausnahmsliste Namen zu schützen und Namen zu verwerfen?



1. Bekannte und eingebürgerte Namen sind gegen minderbekannte Namen zu schützen. — Als eingebürgert sind in erster Linie solche Namen zu betrachten, die in der Zeit etwa von 1830 bis 1890 oder bis 1905 ziemlich allgemein im Gebrauch standen und die sich im angewandt-botanischen Schrifttum, in Lehrbüchern u.dgl. auch weiterhin noch stark erhalten haben. Die Zeit zwischen 1905 und 1950 halte ich nicht für massgebend. Es war eine Zeit des Experimentierens und fortwährenden Wechsels, in der eine richtige Einbürgerung neuer oder neuerdings hervorgeholter Namen kaum möglich war. Ein eingebürgerter Name ist vor allem dann schutzbedürftig, wenn ein älterer unbekannter Name für ihn ausfindig gemacht wurde oder wenn er durch die unselige Homonymieregel (Artikel 61) bedroht ist. Ein älteres Homonym, welches regelwidrig ist oder allgemein aus systematischen Gründen als Synonym angesehen wird, sollte niemals die Ursache sein, dass ein gut eingebürgerter Name ausser Gebrauch gestellt wird. Gut eingebürgerte Namen sind auch dann zu schützen, wenn sie aus sonstigen Gründen den Regeln nicht voll entsprechen, z.B. wenn sie bei ihrer Veröffentlichung nach den jetzt geltenden Regeln überflüssig waren (Art. 60, Punkt 1) oder Eventualnamen darstellten u.dgl.m.; ferner, wenn ihre Bedeutung oder Haupt-Bedeutung nach ihrem Wortlaut oder nach sonstigen Umständen ihrer Veröffentlichung klar ist, sie aber doch später angefochten wurden (z.B. *Cerastium vulgatum* L., die häufigste Art der betreffenden Gruppe, oder *Ribes rubrum* L., die allgemein kultivierte Rote Johannisbeere, *Ulmus campestris* L., die Feld-Ulme), endlich, wenn die Bedeutung erst in einer späteren Veröffentlichung des eigenen Autors voll geklärt wurde und sich nur in diesem Sinne eingebürgert hat (z.B. *Rosa cinnamomea* L. 1759, *Caucalis daucoides* L. 1767, *Orchis latifolia* L.).
2. Zu verwerfen sind Namen, die leicht irreführen können, bes. auch in der angewandten Botanik und im Unterricht (z.B. *Abies Picea* oder das Nebeneinanderbestehen von *Carex Halleri* und *C. Halleriana*, *Lysimachia Hemsleyi* u. *L. Hemsleyana* [Empfehlung XIV]: in solchen Fällen ist natürlich der gebräuchlichste, nicht unbedingt der älteste Name beizubehalten).
3. Zu verwerfen sind Namen, die durch Erweiterung oder Einengung ihres Umfanges eine Bedeutung erlangen oder erlangen würden, die dem ursprünglichen Sinne nicht entspricht (z.B. *Petroselinum crispum*, nur Kraus-Petersilie, würde bei Erweiterung auf *P. hortense* sinnlos werden und ständig irreführen, *Triticum aestivum*, nur

Sommer-Weizen, und *Triticum sativum*, jeder Saat-Weizen, sind für *T. vulgare* nicht anwendbar, weil sie in der Landwirtschaft infolge ihrer Sinnwidrigkeit ständig irreführen würden).

4. Zu verwerfen sind Namen, die auf einem Irrtum des Autors beruhen (Beobachtungsfehler, zufällige Abweichung, mangelhafte Kenntnis wichtiger Umstände), da sie gleichfalls sinnwidrig sind und zu Irrtümern Anlass geben können (z.B. *Carex diandra*, stets dreimännig, *Galinsoga quadriradiata*, normal immer fünfstrahlig). Kein Mensch, der nicht bereits vom Formalismus der Nomenklaturregeln angekränkt ist, wird einsehen können, dass es unmöglich sein soll, derartige Namen abzuschaffen.
5. Zu verwerfen sind Namen, die auf eine Bildungsabweichung begründet sind, auch wenn diese nicht gerade eine Monstrosität im Sinne des derzeitigen Wortlautes des Artikels 65 darstellt (z.B. *Sempervivum Braunii* FUNK, nur die weissblühende Form der erst später richtig erkannten und beschriebenen *S. stiriacum* WETTST., auch das unter Punkt 3 besprochene *Petroselinum crispum* kann hierher gerechnet werden).
6. Zu verwerfen sind Namen, die durch Übertragung des Artnamens aus einer anderen Gattung entstanden und dabei widersinnig oder doch sinnlos geworden sind (z.B. *Potentilla erecta*, sinnlos und mit *P. recta* zu verwechseln, *Potentilla sterilis*). Hierher gehören besonders jene Namen, die den Gattungsnamen mit den Endungen *-oides*, *-inus*, *-formis*, *-florus*, *-folius* u.dgl. wiederholen (z.B. *Phleum phleoides*, *Cerastium Cerastoides*, *Alyssum Alyssoides*, *Hedysarum Hedysaroides*, usw. usw. und *Luzula luzulina*).
7. Zu verwerfen bzw. nur als Sammelnamen beizubehalten sind solche Namen, die von Anfang an als Sammelnamen gedacht waren und sich nur gezwungen oder unsicher auf einen einzelnen Bestandteil bzw. eine Kleinart übertragen lassen (z.B. *Ophrys insectifera*, *Thymus Serpyllum*, *Stipa pennata*, *Festuca ovina*). Der Name *Thymus Serpyllum* ist als Sammelname für die arzneilich verwendeten Kleinarten unentbehrlich. Von den *Thymus*-Spezialisten wurde er aber gerade auf eine solche Kleinart eingeschränkt, die arzneilich wertlos ist. Ein *Thymus*-Spezialist kann leichter umlernen als ein medizinisch-pharmazeutischer Praktiker. Was LINNÉ in erster Linie unter *Stipa pennata* verstanden hat, lässt sich schwer feststellen, wahrscheinlich *Stipa pulcherrima* subsp. *gallica* und nicht *St. Joannis*. — Bei Verwerfung der in den Punkten 2 bis 7 angeführten anfechtbaren Namen wird man in einzelnen Fällen auch solche Namen

- in Gebrauch ziehen müssen, die bisher noch nicht eingebürgert sind.
8. Eine Regelung durch die Artenausnahmsliste ist auch dann empfehlenswert, wenn über die richtige oder zweckentsprechendste Benennung schwer überbrückbare Meinungsverschiedenheiten bestehen.

Manche der in den Punkten 2 bis 7 behandelten Fälle liessen sich auch durch allgemeine Bestimmungen bereinigen, wenn man die Regeln entsprechend abändert oder ergänzt, wie ich zum Teil in meiner Schrift »Vorschläge zur Benennung der Blütenpflanzen Deutschlands« (Fedde's Repert. 50, 1941, 351—361) angeregt habe. Diese Vorschläge möchte ich im Interesse der Allgemeinheit den Fachgenossen dringend zur Beachtung empfehlen. Speziell mit der Frage der Artenausnahmsliste befassen sich meine Schriften: »Anregung zur Schaffung einer Ausnahmsliste für die Namen der Pflanzen-Arten« (Fedde's Repert. 53, 1944, 61—71) und »Die wissenschaftliche Benennung der heimischen Blütenpflanzen und Farne« (Der Biologe, 13, 1944, Heft 3/4, 50—55).

Zum Schlusse betone ich nochmals: Die Regeln samt allen Empfehlungen und Supplementen sowie ihre Durchführungen sollen immer sinnvoll sein. Der Formalismus soll immer von der Vernunft beherrscht werden. Nur dann werden die Regeln im Dienste aller Freunde der Pflanzenwelt ihr Ziel erreichen.

**J. S. L. Gilmour (Director, Royal Horticultural Society's  
Gardens, Wisley, Surrey):**

I am grateful to the Editor for giving me the opportunity of writing a short note on what Dr. A. C. SMITH, in a recent article (*American Journ. Bot.* 36; 624: 1949), has called »a perennial question which has plagued plant taxonomists in recent years«, especially as this question is coming up again, in one form or another, at the Stockholm Congress in July. Having had the privilege of working both among systematic botanists (at Kew) and among horticulturists (at Wisley) I am convinced that the minimization of name changes, of which this problem of *Nomina Specifica Conservanda* is one aspect, is of the greatest importance for the future co-operation between these two branches of plant study.

In the first place, I should make it clear that, although the Royal Horticultural Society has put forward a proposal on the subject at Stockholm, which I shall discuss in this note, the opinions I am expressing are personal ones, and not necessarily those of the Society.

The arguments which have taken place in the past over *Nomina Specifica Conservanda* represent, essentially, a conflict between *producers* and *users*, between taxonomists, who are responsible for the description and naming of plants, and agriculturists, foresters, horticulturists and others concerned with the use of the resulting names. It is natural that most taxonomists should be very reluctant to abandon, even in a limited sphere, the principle of priority which is basic to the *Rules of Botanical Nomenclature* and which has served them so well in their work; but it is equally natural that daily users of names should resent irksome changes, the reasons for which they often understand only imperfectly. Can a solution be found to this long-standing and intractable problem?

I think it can, but not, I suggest, along the well-worn and thorny path of *Nomina Specifica Conservanda*, nor by means of agreed lists of names to be used for a certain period which Dr. SMITH effectively criticises in his article (*loc. cit.*).

In the first place, it is clear that any steps taken to avoid name changes due to the discovery of an earlier synonym or homonym for a species already well-known by a later name must involve the abandonment, in this particular case, of the principle of priority. This principle has, of course, already been abandoned in Art. 21 permitting *Nomina Generica Conservanda*, so that its suspension for specific names would not be a completely new departure. If it can be shown that the objections, on principle, to such a suspension would be outweighed, on balance, by the practical advantages of continued, and improved, co-operation between »producers» and »users», I feel, personally, that the concession would be abundantly worth while. Admittedly this view is based on expediency, which Dr. SMITH (*loc. cit.*) regards as a term of reproach. But are not the whole *Rules* grounded on expediency? Is not the principle of priority itself a matter of expediency, devised by botanists to help them in their work? If it is found, in a particular case, that this principle hinders more than it helps, is it not permissible for botanists, who laid it down, to modify it? Is not Art. 4, setting out »fixity of names» as one of the primary aims of nomenclature, at least as important as Art. 16, dealing with priority?

If this view is accepted there is, nevertheless, I suggest, some objection to establishing *Nomina Specifica Conservanda* as the method of preventing changes in well-known names. A list of conserved names would presumably have to be incorporated into the *Rules* as an appendix, thus giving them a permanency which might possibly be



undesirable. For example, a conserved name might later be shown to be ineffectively or invalidly published. Further, the acceptance, once and for all, of a particular epithet for a particular species, might discourage investigation of its earlier nomenclatural history and thus, perhaps, leave unrecorded facts discovered about it by previous investigators which would be of scientific and historical value.

There is, however, an alternative approach to the problem which is embodied in some of the proposals to be discussed at Stockholm, including that put forward by the Royal Horticultural Society. This approach involves, not the conserving of a particular specific name that would otherwise be rendered illegitimate by an earlier name, but the *exclusion* from nomenclatural consideration of the earlier name, whether synonym or homonym, thus leaving the later name as the legitimate one. The suggestion is not open to the objections (given above) to conserved specific names, and, in particular, as it is the *earlier name* that would have to be put forward for »exclusion», it would have the advantage of drawing particular attention to the existence of this earlier name and thus, not only giving such credit as is due to its author (and discoverer), but recording in permanent form this part of the nomenclatural history of the species.

I will not quote the Society's proposals in full, as they will be available to members of the Congress, but I should like to emphasise that they do, of necessity, involve the reference of names for exclusion (*Nomina excludenda*) to a Committee for recommendation to an International Congress, as is the case at present with *Nomina Generica Conservanda*. Dr. SMITH (*loc. cit.*) sets out some cogent objections to this procedure and admittedly it may not be easy to find botanists with sufficient time and experience who will be willing to undertake the work involved, but there is not, I think, any possible alternative. The task of the Committee, from its nature, will become progressively lighter as time goes on and the experience gained with conserved generic names should be invaluable in carrying out this very similar work. Clearly it should be the policy of those putting forward names for exclusion (as it will undoubtedly be that of the Committee considering them) to exclude only those which, if taken up, would result in the changing of names really long established and widely used. No doubt the Committee would draw up a set of conditions all or most of which a name would have to fulfil if it was to be preserved by excluding an earlier one; for example, currency over a certain period of time, a certain degree of wideness of use and of importance to users,

etc. If these conditions are strictly applied, both by proposers and by the Committee, the number of names put forward for consideration and finally recommended to a Congress would be kept within reasonable bounds.

I think it would be generally agreed that some such proposal as the above is the only practicable alternative to the long term policy of the gradual stabilization of names by bibliographic investigation, involving, undoubtedly, further changes in the names of a considerable number of well known economic plants. In a sense this is the ideal method from the taxonomic point of view, but I am quite convinced that it would lead to increased friction between the »producers» and »users» of plant names which would have serious repercussions on that co-operation between them without which neither can make satisfactory progress.

All who share this view, therefore, will hope that botanists at Stockholm will feel able to stretch out a helping hand to horticulturists and others in allowing the retention of a few well-known specific names by an alteration in the *Rules* on some such lines as I have discussed. I am sure that such a policy would earn large dividends for both pure and applied botany in the future.

I am indebted to Mr W. T. STEARN for help in preparing this note.

**Charles Baehni (Directeur des Conservatoire et Jardin botaniques, Genève). — Le serpent de mer de la nomenclature: les nomina specifica conservanda.**

Sans doute, comparaison n'est pas raison, mais on a quand même le droit et même le devoir de comparer les deux cas des *nomina specifica* et des *nomina generica conservanda*: Ici comme là, il s'agit de limiter les dégâts dûs à l'application stricte du principe de priorité (art. 20) et, pour les premiers comme pour les seconds, on se promet de composer des listes aussi courtes que possible, réduites à l'essentiel.<sup>1</sup>

Là-dessus, j'ai rouvert le 3e édition des Règles et j'ai lu à l'Appendice III la liste des *nomina generica*, une liste que j'ai fréquemment consultée mais que je n'avais jamais lue. J'ai commencé par être saisi d'un saint respect devant tant de science empilée sur tant d'érudition.

<sup>1</sup> LITTLE, E. L., in *Phytologia* 3: 90, 1949. Cf. p. 95. PICHON, M., in *Bull. Soc. bot. France* 96: 216, 1950. Cf. p. 217. JANCHEN, E., in *Fedde Repert.* 53: 61, 1944 et BARTSCH, J. in *Der Biologe* 13, 1944 (t. à p.) ont publié cependant deux premières listes qui concernent 117 espèces pour les seuls pays de langue allemande!

Quelles peines n'a-t-on pas prises pour préserver les *Zoisia* (2—3 espèces), les *Crypsis* (1 espèce), les *Lyginia* (1 espèce) et même les *Zelkova* (4 espèces). Mais mon respect s'est effondré d'un coup lorsque je suis arrivé à la famille des Lauracées devant le genre *Eusideroxylon* TEYSM. et BINN., conservé contre *Salgada* BLANCO. Comme il se fait que je me suis beaucoup occupé des Sapotacées, le nom des *Eusideroxylon* m'était évidemment connu, mais je m'étais borné jusqu'ici à regretter la collision des *Sideroxylon* (Sapotacées) avec les *Eusideroxylon* (Lauracées). Or, je découvre aujourd'hui que les *Eusideroxylon*, si gênants, se composent de 2 espèces dont l'une fournit, je veux bien, le célèbre bois de fer de Bornéo, alors que l'autre n'était pas encore décrite quand le nom du genre a été »conservé« !

Alors, tardivement et inutilement, je me révolte. Comment, on publie des articles, on met en branle le lourd appareil des Congrès, on vote, on imprime des listes, pour imposer au monde un nom aussi malheureux que celui de *Eusideroxylon* et le garder à une espèce? C'est tirer du canon pour se défendre contre les moustiques. Si c'est le but qu'on voulait atteindre en établissant les listes de *nomina generica conservanda*, alors je déclare tout net que ce n'était pas la peine.

Jusqu'ici, j'ai cru que les recueils qu'on réclame à grands cris (trop de cris pour que la cause soit bonne) de *nomina specifica conservanda*, devaient être courts et ne comprendraient que des noms indispensables. Mes yeux se sont arrêtés ces jours-ci sur une liste<sup>2</sup> où l'auteur demande par exemple le maintien du *Rorippa palustris*, du *Primula officinalis* et même, tenez-vous bien, du *Solidago Virga-aurea*. J'en demande pardon à l'auteur distingué de ces listes, mais le *Rorippa islandica*, le *Primula veris* et le *Solidago virgaurea* ne satisfont d'autant mieux que deux, sur trois, sont ainsi nommés dans les flores suisses les plus récentes. Je cherche encore à savoir pourquoi le même auteur voudrait protéger le *Silene inflata* contre le *Silene angustifolia*; il aurait dû plutôt, il me semble, le préserver des attaques victorieuses du *Silene Cucubalus* WIBEL qui est, selon les Règles, le seul nom valable.

Et j'en reviens à ma comparaison dans la liste des *nomina generica*: Si cette liste a été si malaisée à établir, si elle peut actuellement prêter si facilement le flanc à la critique, ne se rend-on pas compte qu'une liste de *nomina specifica* sera beaucoup plus laborieuse à mettre au point, qu'on dressera les uns contre les autres les groupes nationaux ancrés dans des habitudes différentes, qu'on enlèvera enfin toute base

<sup>2</sup> PICHON, l.c.

objective à la nomenclature pour se lancer tête baissée et les yeux bandés dans l'arbitraire.

Si l'on suivait les propositions de MARTIN,<sup>3</sup> on établirait des commissions nationales de nomenclature qui décideraient des noms à garder et des noms à rejeter. Mais je suis sûr que certains pays bien équipés scientifiquement produiront leurs listes nationales de noms à conserver alors que certains autres n'en auront pas les moyens, matériels ou scientifiques. Lorsque les premiers auront achevé leur tâche, ils étendront probablement leur propre juridiction sur les pays moins favorisés. Nous irons tout droit alors vers la dictature scientifique, plus intolérable encore qu'aucune autre.

Ainsi, la Suisse ne possède pas d'espèce de phanérogame endémique, si ce n'est, pour l'instant et à notre extrême frontière, le *Draba ladina*; si elle venait à ériger un tribunal suisse qui déciderait du nom à donner aux plantes de son territoire, il est fort possible que ses décisions ne soient pas acceptées par nos voisins politiques, les Français, les Italiens, les Autrichiens et les Allemands qui ont entre eux tous et sur leur propre sol toutes nos espèces sauf une. Verrons-nous alors un tribunal international, au-dessus des nationaux, prendre des décisions *éventuellement en désaccord avec les Règles internationales*? Ce serait bouffon.

FOSBERG<sup>4</sup> a attiré mon attention sur un excellent article de CORNER<sup>5</sup> où l'auteur démontre que les difficultés ne sont pas tant d'ordre nomenclatural, que d'ordre taxonomique: c'est souvent la méconnaissance des espèces qui entraîne la confusion des noms. Pour avoir travaillé depuis 20 ans dans un grand herbier et constaté presque tous les jours que ce sont les espèces les plus répandues, les plus cultivées ou les plus vulgaires qui y sont — proportionnellement et même absolument — le plus mal représentées, j'en arrive à ceci: il serait du devoir de ceux qui se plaignent de l'instabilité de la nomenclature, c'est à dire des horticulteurs, des forestiers, des phytopathologistes, de récolter en abondance des matériaux, de les envoyer, avec leurs notes et leurs observations, à plusieurs herbiers du monde. Les travaux de morphologie, de taxonomie et de nomenclature qui naîtraient de cette coopération feraient plus pour la stabilisation des noms que toutes les décisions des Congrès. Et je voudrais reproduire ici les mots mêmes qu'emploie FERNALD pour montrer, à propos du *Pinus palustris*, l'importance fondamentale de l'étude des spécimens eux-mêmes, avant toute décision

<sup>3</sup> MARTIN, A. C. in Amer. Midl. Nat. 34: 800, 1945.

<sup>4</sup> FOSBERG in Rhodora 52: 7, 1950.

<sup>5</sup> CORNER, E. J. H. in Gard. Bull. Straits Settl. 10: 56, 1939.



concernant les noms: Those who earnestly wish conservation of really very important names of economic plants should proceed with care, looking out that their would-be conserved names rest upon undoubted types. The seeking out of types and their conscientious study is an exacting task, neglected by many, but conservation based on accumulated errors, such as surrounded all the early accounts of *Pinus palustris*, is not worth the name. We are not, as scientists, aiming to perpetuate error.<sup>6</sup>

Enfin, vouloir fixer *arbitrairement* des noms en se fondant sur les variations que certains d'entre eux ont subies depuis 50 ans, c'est mettre la charrue devant les boeufs. Car les ressources cachées des bibliothèques vont tout de même en s'épuisant et plus nous allons de l'avant, plus les noms ressuscités seront rares et dans 50 ans, si nous ne touchons pas aux »Règles», une stabilité presque parfaite sera certainement obtenue.

En revanche, si nous perçons la digue de la priorité pour arroser la petite plate-bande des malcontents, nous verrons la liste s'allonger, je veux dire le petit trou s'agrandir, la digue crèvera et le flot des revendications emportera la plate-bande, le jardin et la maison.

Il ne restera plus aux botanistes qu'à recommencer; mais alors, fussent-ils tous des Linnés de génie, personne ne les prendra plus au sérieux.

### Professor C. Skottsberg (Gothenburg):

That many experienced and conscientious botanists have found it highly desirable to conserve a number of specific epithets clearly shows that there is something wrong with the Rules. As long as we are forced to take up a name never used by anybody except its author and reject the name commonly used by everybody and found in innumerable publications, as long as the long-established name of a wellknown species (a) must be transferred to another species (b), the present name of which has to be dropped or, if the enthusiastic name-changer is lucky, can be attached to a third species (c), the name of which, and so forth . . . — the new name of (a) may affect a fourth species (d) — as long as such chain reactions, based on the Rules, and causing more confusion than any *nomina confusa* or *nomina ambigua*, occur, the need for more stability is felt by those who do not love change for change's own sake.

The same may be said of many ridiculous combinations where,

<sup>6</sup> FERNALD, M. L. *Rhodora* 56: 241, 1948.

most likely in all cases, a normal but younger specific name is available making the creation of a new one superfluous, and of the nonsensical, perhaps even hideous orthographic errors, due either to ignorance or to a slip of the pen but now regarded as sacrosanct — most likely their authors would have thanked you if you had had a chance to correct them.

As the Rules are, it is too easy to find a pretext for a name-change. Modify them, make them more practical and thus less objectionable and nobody will ask for *nomina specifica conservanda*.

## Litteratur.

**International Rules of Botanical Nomenclature.** Formulated by the International Botanical Congresses of Vienna, 1905, Brussels, 1910, and Cambridge, 1930. Adopted and revised by the International Botanical Congress of Amsterdam, 1935. Compiled from various sources by W. H. CAMP, H. W. RICKETT and C. A. WEATHERBY. Unofficial special edition issued as a service to members of the American Society of Plant Taxonomists. 1948. Second printing, reproduced by Offset and Published by the Chronica Botanica Co. Waltham, Mass., U.S.A. for the New York Botanical Garden, and the American Society of Plant Taxonomists. (Sep. ur: Brittonia, Vol. 6, No. 1, pp. 1—120, 1947.)

På den sista internationella botanistkongressen hittills — den sjätte, i Amsterdam 1935 — antogs åtskilliga, i huvudsak dock föga ingripande förändringar och tillägg till de då gällande internationella reglerna för den botaniska nomenklaturen, vilka i sin tur fått sin sista utformning på närmast föregående kongress, i Cambridge 1930. Dessa Cambridge-regler hade först 1935 kunnat publiceras i tryck; denna regelupplaga, den tredje i ordningen, utkom hos Fischer i Jena med text på engelska, franska och tyska och är alltså den sista officiella. Det var givetvis avsikten, att en motsvarande fjärde upplaga, innehållande reglerna i den lydelse, de erhållit i Amsterdam, snarast möjligt skulle iordningställas och publiceras. Av olika orsaker blev dock redigeringsarbetet fördröjt, och kriget lade sedan definitivt hinder i vägen för utgivningen. Den enda möjligheten för den som ville ha reda på den faktiskt gällande lydelsen av reglerna var därför att ur Amsterdam-kongressens tryckta redogörelse plocka ut de antagna förändringarna, en för de flesta ej eller blott med svårighet användbar metod och besvärlig även för den som har tillgång till denna publikation. Härtill måste också läggas den lista över nyantagna *nomina generica conservanda*, som publicerats i Kew Bulletin 1940, och den sammastädes 1936 meddelade förteckningen över *nomina familiarum conservanda*.

För att avhjälpa denna brist vidtog den tämligen nybildade men inte minst på nomenklaturens område livligt verksamma sammanslutningen av amerikanska systematiker, American Society of Plant Taxonomists, den prisvärda åtgärden att sammanställa dessa ändringar och tillägg och infoga dem i förutvarande regelupplaga till en sammanhängande text och att publicera denna i tryck, i tidskriften Brittonia 1947. Då denna publikation givetvis

väckte stort intresse även utanför nämnda krets och behovet var allmänt av en sådan sammanfattning, föranstaltade *Chronica Botanica* ett nytryck i offset, vilket finnes tillgängligt i bokhandeln, inbundet i gott klotband. Denna — som man är angelägen att påpeka — inofficiella nya upplaga innehåller endast den engelska texten; denna är dock numera normalversionen. De textstycken, som genom beslut i Amsterdam tillagts eller erhållit ny lydelse, ha markerats med halvfet stil och falla sålunda omedelbart i ögonen.

Typografiskt är upplagan mycket sober och på grund av sitt mindre format och bättre papper betydligt trevligare att handskas med än tredje upplagan. Till dess större hanterlighet bidrar också, att de båda listorna över *nomina generica conservanda* för blomväxter i 1935 års regler (dels den över redan antagna namn, dels den med föreslagna sådana) nu hoparbetats till en enda, där släktena (ordnade efter DALLA TORRE & HARMS) också fått en mera överskådlig typografisk anordning. Denna lista utgör en del av det appendix III, där man nu samlat samtliga såväl antagna som föreslagna längder över *nomina conservanda* inom de olika större grupperna; dessa ha ordnats som 10 skilda avdelningar, motsvarande växtrikets huvudgrupper, varvid i inledningen till varje avdelning angetts, om förtecknade namn endast föreslagits till konservering eller verkligen antagits. I fråga om vissa alggrupper, där redan före 1935 en del *nomina conservanda* funnos, ha dessa jämte de senare föreslagna men ännu ej antagna namnen hoparbetats i en enda lista, varvid den senare kategorin utmärkts med särskilda tecken, så att ingen förväxling kan ske. Släktnamnen ha inom varje sådan kryptogamgrupp ordnats alfabetiskt, men varje avdelning följs av en alfabetisk familjeförteckning med uppgift om vart de behandlade släktena höra. Hela detta appendix åtföljes av ett utomordentligt kärkommet register över såväl *nomina conservanda* som *nomina rejicienda* inom samtliga grupper. Ett annat appendix upptar de nyssnämnda *nomina conservanda* för familjer. Slutligen har också denna nya upplaga försetts med ett engelskspråkigt register, som visserligen av utrymmesskäl måst göras ganska begränsat men som genom sin redighet är av stor nytta och ersätter det svårhanterliga franska register, som varit det enda hittills.

Om det också kan antas, att reglerna genom sommarens kongress komma att underkastas väsentliga ändringar, är det dock alltid nödvändigt att ha tillgång till 1935 års version. För detta ändamål kan den nu refererade upplagan utan tvekan rekommenderas, helst som det kan synas tivelaktigt, huruvida det ens kan vara någon idé att så långt efteråt som efter Stockholmskongressen utge en officiell version av regler, som då ej längre gälla oförändrade. De små avvikelser, som möjligen kunna förefinnas mellan den amerikanska upplagan och den officiella lydelsen, borde ju på något enklare sätt kunna göras tillgängliga och så av den intresserade föras in i hans exemplar av den förra. Även om — som man får hoppas — resultatet av den sjunde botanistkongressens nomenklatoriska arbete kan offentliggöras i form av en ny regelupplaga betydligt snabbare än fallet var efter de båda senaste kongresserna, måste det ju ändå dröja en ganska avsevärd tid, innan denna kan se dagens ljus och kan ersätta 1935 års bestämmelser.



STEPHENSON, MARJORY: *Bacterial Metabolism*. Third edition. Pp. XIV+398, with 1 plate and 81 figures. Longmans, Green and Co., London, New York, Toronto 1949. 30 s. net.

I förordet till tredje upplagan av sin bok *Bacterial Metabolism* framhåller framlidna författarinnan MARJORY STEPHENSON, att den vetenskap, som sysslar med bakteriernas ämnesomsättning, nu svällt ut till sådana proportioner, att det icke längre är möjligt för en människa att behärska alla dess grenar. Samtidigt som man är benägen att ge författarinnan rätt, kan man icke undgå att beundra det sätt på vilket hon bemästrar det nya vetandet på detta område. Sedan bokens första och andra upplaga utkom 1930, resp. 1939, har en flod av undersökningar berikat mikrobiologien, kanske framför allt tack vare biokemiens och biofysikens snabba framsteg. Läran om bakteriernas ämnesomsättning har blivit en gren av biokemien. Bland de många nyheter, som tillkommit under det sista årtiondet, märkes framför allt införandet av isotoptekniken, som spritt nytt ljus över gamla svårförståeliga fakta, såsom koldioxidens reduktion till metan eller uppdagat helt nya fenomen, såsom den i de levande organismerna allmänt förekommande koldioxidfixeringen. Den mikrobiologiska genetiken, bildningen av adaptiva enzym, tillväxtämnenas funktion samt förekomst och funktion av antibiotika äro andra gebit, som bidragit till att på kort tid vidga och omdana denna vetenskap. Det är under sådana omständigheter föga underligt, att författarinnan varit tvungen att omarbета och nyskriva åtskilliga av kapitlen från tidigare upplagor.

Det är icke recensentens mening att här ge en detaljgranskning av boken. De elva kapitlen behandla bl.a. respiration, jäsning, kväve- och nukleinsyresomsättning samt näringsämnen och tillväxt. Genom att boken icke är ensidigt medicinskt inriktad och genom en god avvägning av de olika partierna blir den av stort värde även för de discipliner, som stå mikrobiologien nära, icke minst växtfysiologien. Särskilt gäller detta de tämligen utförliga kapitlen om fixering av atmosfärens kväve samt om autotrofa bakterier och bakterier med fotosyntes. Dessa kapitel fyller på ett utmärkt sätt de luckor man kan finna i den anglosachsiska växtfysiologiska lärobokslitteraturen, där dessa partier ofta får en väl styvmoderlig behandling. I slutkapitlet om enzymernas variation och adaptation behandlas även nyare arbeten om enzymadaptation inducerad genom miljöförändringar. Boken avslutas med en utförlig bibliografi, som ytterligare förhöjer dess värde.

SVEN ALGÉUS.

LØDDESØL, AASULV og LID, JOHANNES, *Myrtyper og Myrplanter*. Grøndahl og Søns Lantbruksskrifter Nr. 39. Grøndahl & Søns Forlag. Oslo 1950. 95 sid. 100 ill., därav 71 teckningar av DAGNY TANDE LID.

Denna skrift utgör en reviderad upplaga i bokform av en som särtryck utgiven artikelserie »Botaniske holdepunkter ved praktisk myrbedømmelse» i »Meddelelser fra Det norske myrselskap». Den är främst avsedd för norska jordbrukare och skogsmän vid bedömning av myrar för odling eller skogsdikning. Huvuddelen av boken upptas av beskrivningar av 100 myrväxter: 43 gräs och halvgräs, 15 örter, 13 ris och buskar, 14 vitmossor och 15 blad-

mossor. Beskrivningarna äro pregnanta och klara. Kärleväxterna bli utmärkt karakteriserade med hjälp av teckningarna. Dessa, som utförts av DAGNY TANDE LID äro av samma höga kvalitet som i LIDS »Norsk Flora». Uppgifter om ståndort, utbredning i Norge och krav på underlagets näringshalt fullständiga bilden av varje art. Det är intressant att kunna konstatera, att uppgifterna om arternas näringskrav mycket väl överensstämma med förhållandena i Syd- och Mellansverige. Ett och annat undantag finns, t.ex. *Carex magellanica*, som enl. svensk erfarenhet ej kan rubriceras som »kravfull till middels kravfull». Den hör utan tvekan till våra anspråkslösaste myrväxter.

Vid behandlingen av myrtyperna redogöra författarna för tidigare norska myrindelningar av LENDE-NJAA, HOLMSEN och THURMAN-MOE. De följa i den redogörelse för myrtyperna och deras praktiska användbarhet och bonitet, som avslutar boken, HOLMSENS indelning med smärre ändringar. De härvid urskilda huvudtyperna: »Mosemyrer, grasmyster, lyngmyrer, krattmyrer og skogmyrer», äro uppställda efter de fysiognomiskt dominerande arternas allmänna livsform. Även den finare indelningen göres efter de fysiognomiskt dominerande typerna. Så uppdelas »Mosemyrer» i vitmossmyrar och *Rhacomitrium*-myrar (speciella för Västanorge) och var och en av dem i ljungrika och gräsrika. De av gräs dominerade myrarna indelas i rena gräsmyrar, starrmyrar, *Juncus*-myrar och *Eriophorum-Scirpus caespitosus*-myrar. De båda förstnämnda motsvara våra svenska kärr, medan de båda sista troligen mest överensstämma med de sydvästsvenska fukthedarna, vilka även HOLMSENS »Lyngmyrer» stå nära. För att få fram praktiskt lätt urskiljbara och även i fråga om torvslaget någorlunda enhetliga myrtyper för ett område av sådan storlek och med så skiftande natur som Norge är troligen ett i huvudsak fysiognomiskt system sådant som författarna använt det enda möjliga.

För en svensk läsare ger det föreliggande arbetet en god bild av de norska praktiska myrindelningarna och värdefulla uppgifter om norska myrväxters ekologi och utbredning.

TORSTEN HÅKANSSON.

STRASBURGER-KOERNICKE: Das kleine botanische Praktikum für Anfänger. XI. Aufl. von MAX KOERNICKE. Jena, Gustav Fischer 1949. 12 Mk.

Den elfte upplagan av STRASBURGERS lilla Praktikum ansluter sig i allt väsentligt till närmast föregående upplagor. Vissa förbättringar och mindre utvidgningar ha dock gjorts. Så ha en del figurer ersatts med nya; särskilt bör nämnas, att detta är fallet med de illustrationer, som visa kärndelningens förlopp i mitos och meios. I fråga om cytologiska metoder har det tillkommit en rätt utförlig redogörelse för snabbmetoderna vid fixering enligt Heitz och Geitler, och likaså för färgningsförfarandet enligt Feulgen-metoden. På grund av tidsförhållandena ha givetvis uppgifterna om anskaffning av apparatur och utensilier och kostnaderna härför måst inskränkas. Det är emellertid glädjande att en ny upplaga kunnat utkomma av denna bok. Den utgör en mycket god handledning för dem som idka självstudier i olika växtgruppers anatomi, liksom för alla som undervisa i ämnet.

H. HJELMQVIST.



## Notiser.

**Lunds Botaniska museum.** Assistenten vid Naturhistoriska riksmuseets botaniska avdelning, fil. dr TYCHO NORLINDH har utnämnts till 1:ste museiintendent vid Botaniska museet i Lund fr.o.m. den 1 maj 1950.

**Doktorsdisputation.** För vinnande av filosofie doktorsgrad vid Uppsala universitet försvarade fil. lic. STEN SELANDER den 24 maj 1950 en avhandling med titeln: Floristic Phytogeography of South-Western Lule Lappmark.

**Forskningsanslag.** K. Fysiografiska sällskapet i Lund har vid sammanträde den 4 april 1950 utdelat bl.a. följande anslag: Fil. mag. fru ELSA KYLIN för fullföljande av professor H. KYLINS odlingsförsök med mikroskopiska och submikroskopiska alger 300 kr.; fil. lic. SIGVARD LILLIEROTH och fil. mag. fru GUNVOR LILLIEROTH för botaniskt-limnologiska undersökningar i Helgeån 500 kr.; professor HERIBERT NILSSON för en undersökning över bastardebildning och variabilitet inom släktet *Salix* i nordöstra Skåne 400 kr.; sektionen Skånes Flora för fortsatt inventeringsarbete 800 kr. — Stiftelsen Lars Hiertas Minne har utdelat följande anslag till botaniska forskningar: Docent NILS ALBERTSON för undersökning av vissa växtsamhällen i den öländska alvarvegetationen 800 kr.; fil. lic. MAGNUS FRIES för en avhandling om den senkvartära vegetationsutvecklingen i mellersta Bohuslän och angränsande delar av Dalsland 1 950 kr.; fil. lic. ALF LILJEFORS för undersökningar över embryologi, cytologi och artbildning inom släktet *Sorbus* 2 500 kr. — Statens naturvetenskapliga forskningsråd har vid sammanträde den 6 maj 1950 utdelat bl.a. följande anslag: Fil. dr ASTRID CLEVE VON EULER för tryckning av en svensk-finsk diatomacéflora 8 000 kr.; professor HANS BURSTRÖM för undersökning av svavelomsättningen hos högre växter, i första hand vete, 5 200 kr.; professor HERIBERT NILSSON för fortsatta undersökningar av bastarderingsförhållanden och komplex bastardebildning inom släktet *Salix* 2 700 kr.; laborator AXEL NYGREN för fullföljande av undersökningar över apomixis hos växter 4 320 kr. — Ur fonden för skoglig forskning har den 24 maj 1950 beviljats bl.a. ett anslag på 35 000 kr. till professor HOLGER ERDTMAN för att tillsammans med docent E. RENNERFELT undersöka kemiska och mikrobiologiska faktorerers inverkan på skogsträdens vitalitet och resistens mot röt-svampar.

**Botanistkongressen i Stockholm.** Till den 7:e internationella botaniska kongressen i Stockholm i juli 1950 äro c:a 1 400 deltagare anmälda. De länder som äro starkast representerade, äro England och Sverige, i tredje rummet kommer U.S.A., därefter Holland. Tyskland och Frankrike sända ungefär lika många representanter. Även från så avlägsna länder som Nya Zeeland, Japan och Ecuador äro deltagare anmälda.